THESIS

THE INFLUENCE OF DIET, HABITAT, AND RECREATIONAL SHOOTING OF PRAIRIE DOGS ON BURROWING OWL DEMOGRAPHY

Submitted by

Jason Daniel Woodard

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WE HEREBY RECOMMEND THAT THE THESIS PREPARED UNDER OUR SUPERVISION BY JASON DANIEL WOODARD ENTITLED THE INFLUENCE OF DIET, HABITAT, AND RECREATIONAL SHOOTING OF PRAIRIE DOGS ON BURROWING OWL DEMOGRAPHY BE ACCEPTED AS FULFILLING IN PART REQUIREMENTS FOR THE DEGREE OF MASTER OF SCIENCE.

Committee on Graduate Work

Adviser

Department Head (GDPE)

ABSTRACT OF THESIS

THE INFLUENCE OF DIET, HABITAT AND RECREATIONAL SHOOTING OF PRAIRIE DOGS ON BURROWING OWL DEMOGRAPHY

The burrowing owl is a ground-nesting raptor that is in decline across much of its geographic range. Habitat loss and widespread control of fossorial rodents on which burrowing owls regionally rely for nest sites are the primary contributors to owl decline. In addition to reducing breeding and foraging opportunities, habitat loss and eradication programs may result in suboptimal habitat conditions at remaining sites. Identifying the habitat characteristics preferred by burrowing owls and the prey important to successful reproduction are top priorities. Human activity may exacerbate declines in local breeding populations. Isolating and mitigating sources of disturbance to nesting owls is a critical step in achieving conservation goals.

Black-tailed prairie dog colonies are frequently occupied by burrowing owls where ranges overlap. In northeastern Colorado, prairie dog colonies provide the majority of suitable nesting habitat. I studied a population of burrowing owls nesting on the Pawnee National Grassland, Weld County, Colorado, to determine how prey use and nest placement affect demography. Specifically, my objectives were to (1) describe local prey use, compare the owl's diet across its geographic range, and relate diet measures to reproduction; (2) identify the habitat features that drive nesting patterns, and evaluate the

reproductive consequences of nest placement; and (3) identify the factors influencing recreational shooting of black-tailed prairie dogs, and relate burrowing owl breeding numbers and reproductive output to the presence and intensity of shooting activity.

Owls foraged opportunistically for invertebrate prey, using readily available sources to supplement intake of more profitable vertebrate species. Vertebrate use was low and decreased throughout the breeding cycle. Consumption rates may have met minimum dietary levels necessary to initiate nesting, but may not have been sufficient to benefit breeding owls through increased biomass gains. Invertebrates comprised the majority of the diet, a theme common to most diet studies. Their ready abundance and availability provided owls with an attractive alternate food source, and may have buffered owls against the reproductive consequences of short-term food shortage.

Nearest-neighbor distance and satellite burrow density were poor predictors of nest placement. Habitat-based models explained little variation in reproductive performance at the nest level. Annual variation was significant. Nesting pairs in 2000 had a higher probability of success and fledged more young per breeding attempt than did their 1999 counterparts. Increased rates of starvation and flooding may have contributed to lower reproduction in 1999.

Prairie dog colony size moderately influenced breeding densities and colony reproductive performance. Large colonies supported lower breeding densities, were less successful, and fledged fewer young per breeding attempt than did small colonies. Small colonies may constitute superior habitat if breeding densities are indicative of site quality. High rates of landscape fragmentation and human disturbance may have reduced reproductive performance on large, public sites. Burrow availability did not limit

breeding densities, but it may have provided a source of refuge and prey to nesting pairs. No effect of prairie dog activity on measured demographic parameters was evident.

Land ownership primarily governed recreational shooting patterns. Shooters did not demonstrate strong preferences for specific colony characteristics, using the majority of available public sites. Colonies subject to recreational shooting activity supported more breeding owls, but nests had lower success rates and fledged fewer young than did nests on colonies not exposed to shooting activity. Reproduction did not exhibit a linear response to recreational shooting intensity suggesting other factors contributed to reproductive variation. Adult owl mortality from recreational shooting invariably resulted in nest failure. Although gunshot trauma was infrequent, the additive effects of breeder loss and reduced reproductive output remain a cause for concern.

Increasing the number of small, expanding prairie dog colonies will provide prospective breeders with potentially productive sites. As burrowing owls occupy the majority of colonies on the Pawnee National Grassland, many sites are likely to support nesting pairs. Maintaining a sizable pool of breeders will help to minimize the effects of annual reproductive variability and episodic plague on population viability. Protecting important vertebrate and invertebrate prey sources and reducing shooting activity on colonies historically productive or preferred by burrowing owls are essential to effective management. Incorporating reproductive, survival, and recruitment data into monitoring efforts will provide managers with a clearer picture of overall breeding conditions.

Jason Daniel Woodard
Graduate Degree Program in Ecology
Colorado State University
Fort Collins, CO 80523
Spring 2002

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CHAPTER 1

INTRODUCTION

BACKGROUND

The burrowing owl (*Athene cunicularia*) is a ground-nesting raptor found in western North America, Central America, South America, and locally in Florida, the Bahamas, and the Dominican Republic. Currently, the burrowing owl is a listed endangered species in Canada (Wellicome and Haug 1995) and has federal threatened status in Mexico (Holroyd et al. 2001). Although the owl has received no federal classification in the United States, many local and regional populations have experienced declines, prompting the owls' listing as a species of concern (Sheffield 1997, Holroyd et al. 2001).

The net loss, degradation, and fragmentation of habitat are believed to be primary contributing factors to regional population declines (Butts 1973, Wellicome and Haug 1995, Clayton and Schmutz 1999). Agricultural and urban development has transformed the once-extensive grassland prairie into one of the most modified and endangered ecosystems worldwide (Rowe 1987, Sampson and Knopf 1994, Coppedge et al. 2001). At present, <25% of the Canadian grasslands remain in native vegetation (Holroyd et al. 2001). Degradation and fragmentation of the landscape may compound impacts on population persistence by reducing the suitability and profitability of remaining habitat

patches. Increased breeder susceptibility to "edge effects" such as predation has been reported in avian species (Wiens 1994, Howard et al. 2001). Although generalist species may benefit from grassland fragmentation (Johnson and Igl 2001), many species associated with the grassland ecosystem have decreased, some precipitously (Sampson and Knopf 1994, Coppedge et al. 2001). Raptor species such as the western burrowing owl (*A. c. hypugaea*) may be particularly vulnerable to habitat effects. Schmutz (1989) observed ferruginous hawk (*Buteo regalis*) declines at low to moderate levels of fragmentation (>30% cultivation). Reductions in short-eared owl (*Asio flammeus*) populations are also reported (Holroyd 1996).

Declines in the western burrowing owl may be strongly associated with its ground-nesting behavior. Although capable of nest excavation (Thomsen 1971, Keller and Vanegas 1998), density data suggest regional dependence on fossorial rodents for nest sites (Pezzolesi 1994). Occupation of black-tailed prairie dog (*Cynomys ludovicianus*) colonies is common where ranges overlap (Desmond 1991). Habitat loss, poisoning, sylvatic plague (*Yersinia pestis*) and recreational shooting have reduced black-tailed prairie dogs to approximately 2% of their former population size (Miller et al. 1994). Control of rodent populations may reduce nest-site availability and eliminate potentially valuable prey sources of foraging owls and other associate species. The net loss of prairie dogs has eliminated the prey base of the black-footed ferret (*Mustela nigripes*), prompting precipitous population declines and the ferrets' eventual extinction in the wild (Biggins et al. 1993). Elimination of prairie dogs, an ecosystem engineer whose grazing and clipping maintains low vertical vegetation structure (Bonham and Lerwick 1976), has reduced colony suitability for ground-nesting species like the

mountain plover (*Charadrius montanus*) (Knowles et al. 1982) and burrowing owl (Green and Anthony 1989). Rapid burrow degradation following prairie dog extirpation leads to colony disuse by nesting owls within 1-3 years (Butts 1973).

Long-term persistence of the burrowing owl remains questionable across much of its range (Clayton and Schmutz 1999, Holroyd et al. 2001). Although habitat destruction and alteration are the likely main causes of continued population declines (Uhmann et al. 2001), habitat effects alone cannot explain why the Florida subspecies (*A. c. floridanus*), is showing similar population collapses despite a recent expansion of its breeding range (Ligon 1963). Isolating additional sources of decline, including the role human activity plays in nest placement and reproductive determination, and improving collaboration and educational outreach will be particularly important to effective conservation.

DIET

Burrowing owls are opportunistic foragers and dietary generalists (Green et al. 1993, Silva et al. 1995). Although invertebrates and small mammals are the preferred prey, burrowing owls will exploit a diverse prey base, including bats, birds, and reptiles when and where abundant (Schlatter et al. 1980, Wiley 1998, Hoetker and Gobalet 1999). Invertebrates are most frequently consumed as prey, but typically contribute little to overall prey biomass (Gleason and Craig 1979, Thompson and Anderson 1988). High levels of invertebrate consumption may be the product of widespread invertebrate abundance and availability and the burrowing owls' penchant for ground foraging (Schlatter et al. 1980, Grimm et al. 1985). Numerous diurnal trips near the nest mound have been reported and invertebrate prey are almost exclusively the target (Marti 1974, Plumpton 1992).

Vertebrates are a rich source of dietary protein and moisture (Pezzolesi 1994). Delayed numerical responses to small mammal populations (Silva et al. 1995, Poulin et al. 2001), and elevated levels of nesting success and productivity during a vole outbreak (Poulin et al. 2001) suggest vertebrate prey are an important dietary component; however, vertebrate intake decreases through the breeding season (MacCracken et al. 1985, Schmutz et al. 1991). Dietary shifts may reflect seasonal changes in prey abundance (Green et al. 1993), or may be a response to the demands associated with rearing young (Errington and Bennett 1935). Wellicome (2000) indicated the nestling phase frequently is food-limited. A shift to invertebrate prey sources may provide owls and their young with a constant, albeit reduced, food source, and may increase nest attendance during critical phases of the breeding cycle.

NEST SITES

Multiple burrow types are used for nesting, including those excavated by badgers (*Taxidea taxus*) (Green and Anthony 1989), ground squirrels (*Spermophilus* spp.) (Martin 1973, Konrad and Gilmer 1984), desert tortoises (*Gopherus flavomarginatus*) (Rodriguez-Estrella and Ortega-Rubio 1993), yellow-bellied marmots (*Marmota flaviventris*) (Rich 1986), and black-tailed prairie dogs (Plumpton and Lutz 1993, Desmond and Savidge 1996). Burrowing owls also utilize rock outcrops (Rich 1986) and "urban" burrows on occasion; nests on airports (Thomsen 1971), in drainage pipes (Botelho and Arrowood 1996), and under roof eaves (Zambrano 1998) are noted. Even scrap-lumber roosts may provide suitable nesting habitat (Grier 1997).

The burrow is the functional breeding unit, providing a sheltered environment for breeding, and serve as a critical refuge from predators and severe weather. Invertebrate

species may frequent the burrow system (Borror et al. 1989). If owls utilize these prey sources as Green and Anthony (1989) suggest, burrows may also provide a reliable food source during adverse conditions. Although return rates in migratory populations are low, reuse of burrows by those that do return indicates nest placement is in part a result of selection for specific burrow and habitat attributes (Lutz and Plumpton 1999).

Nest-site selection has been studied in relation to numerous burrow criteria, including: burrow orientation and slope; burrow diameter and length; vegetation height and vertical structure; and soil texture (MacCracken et al. 1985, Rich 1986, Plumpton and Lutz 1993, Rodiguez-Estrella and Ortega-Rubio 1993, Toombs 1997). Comparisons between nest and random burrows have yielded few consistent patterns. Vegetation height and cover data show the strongest trends. Owls nest in areas of short, sparse cover where increased horizontal visibility facilitates detection of predators and/or prey (MacCracken et al. 1985, Green and Anthony 1989). Toombs (1997) observed a general avoidance of sandy soils by burrowing owls breeding in southeastern Colorado. Owls may avoid burrows of this texture because they are inherently unstable and prone to rapid degradation (Desmond et al. 2000). However, since it is the prairie dog that is actively selecting for suitable burrowing media, owl soil preferences may simply be an artifact of prairie dog colony location.

Nest placement may depend not only on some physical property of the burrow itself, but also on the nature of the habitat surrounding the nest mound. Burrowing owl nests frequently are surrounded by a number of accessory burrows. These "satellite" mounds are used by adults and young as refuge (Henny and Blus 1981, Konrad and Gilmer 1984), and are integral to juvenile dispersal (King and Belthoff 2001). Owls may

select areas providing maximum cover and dispersal opportunities. Selection decisions of other breeding birds may determine the spatial distribution of nests. If the location of neighboring nesting pairs promotes competition for limited resources, birds should adjust nest placement to minimize fitness impacts (Powell and Steidl 2000). Distance to neighboring conspecifics has been linked to desertion and lower reproductive success in burrowing owls (Green and Anthony 1989, Griebel 2000).

COLONY SELECTION

Burrowing owls nesting in colonial sciurid habitat frequently must select a colony in which to breed. Occupation rates are quite high; however, colonies are not used equally. As in nest-level studies, horizontal visibility appears to be a key determinant of nesting patterns (MacCracken et al. 1985, Green and Anthony 1989). Although vegetative clipping by prairie dogs is characteristic of active colonies, subtle differences in vegetation height and composition can influence occupation rates, determining which colonies will or will not support breeding owls (Plumpton and Lutz 1993).

Coulombe (1971) suggested burrow availability as a limiting factor to population size. In low burrow density habitats, such as pastures containing badger burrows ($\bar{x}$ = 1.8 burrows/ha; Green and Anthony 1989), the lack of abundant nest and satellite mounds may limit the availability of suitable nesting habitat. In contrast, areas of high burrow density may provide additional breeding opportunities, supporting larger populations and higher breeding densities. Whether higher burrow densities on prairie dog colonies preclude burrow availability effects remains to be seen. Preferential (Plumpton and Lutz 1993) and non-selective (Desmond and Savidge 1996) use of high burrow density habitat indicates burrow availability may be a factor of local importance.

Numerous studies have documented an effect of colony size. Larger colonies are more likely to be occupied, and support higher numbers of nesting pairs (Toombs 1997, Ekstein 1999, Desmond et al. 2000) but lower breeding densities (Hughes 1993). Occupation of large colonies may result from exclusion at preferred breeding sites if density is indicative of habitat quality. Nest placement along the colony perimeter is reported (Butts 1973, Hughes 1993, Desmond et al. 1995). Although owls may be keying in on profitable prey sources along the colony boundary and in adjacent habitats, it is possible that owls are selecting for the high prairie dog activity characteristic of the colony perimeter (Hughes 1993).

LANDSCAPE FACTORS

Landscape can influence burrowing owl nesting patterns at several scales of resolution. At a coarse scale, the geographic distribution and abundance of nest-providing populations establishes potential habitat. Although nest excavation is possible, owls are primarily limited to areas offering abundant nesting opportunities. Differences in the composition or configuration of habitat around potential sites may regulate occupancy rates, nesting densities, and reproduction. Owls have demonstrated preferences for specific habitat complexes (Rich 1986, Rodriguez-Estrella and Ortega-Rubio 1993), and colonies in moderately fragmented landscapes (Millsap and Bear 2000, Orth and Kennedy 2001). Increased nest success rates in Florida habitats of 50-60% development indicate that owls may benefit reproductively by such decisions (Millsap and Bear 2000); however, fragmentation effects on occupancy or demography will vary with the habitat structure, landscape context, and predator/prey community composition of the local environment (Tewksbury et al. 1998).

Prey availability may contribute to observed patterns of owl habitat selection and nest placement in shortgrass and shrubsteppe habitats (Rich 1986, Green and Anthony 1989, Desmond et a. 1995); however, supportive prey-based data are lacking. Burrowing owls have shown a preference for (Butts 1973, Rich 1986) and avoidance of (Haug and Oliphant 1990) cropland habitat. Although the consensus is that cultivated lands house an abundant prey base, dense vegetation may limit prey availability to foraging individuals (Bechard 1982). Because vegetation structure and prey demography in agricultural habitats are likely to vary spatially and temporally, habitat-use patterns may be based on periodic assessments of cropland profitability.

REPRODUCTION

Burrowing owls lay a single clutch of 6-11 eggs (Bent 1938); double brooding is reported but rare (Millsap and Bear 1990, Gervais and Rosenberg 1999). Clutch size is correlated with nest initiation date in migratory populations. Pairs arriving and initiating nests early in the breeding season lay more eggs on average than late-season pairs (Griebel 2000). Clutch size varies with geographic location; however, annual variation within sites may be quite small.

Nesting success and fledging rates also differ among breeding populations. Reported success rates include: 53% in Idaho (Green and Anthony 1989); 54% in California (Thomsen 1971), 60% in Durango, Mexico (Rodriguez-Estrella and Ortega-Rubio 1993); 70% in Florida (Millsap and Bear 2000); and 100% in New Mexico (Martin 1973). Likewise, fledging rates vary from lows of approximately 1.3 young (Rodriguez-Estrella and Ortega-Rubio 1993) and 1.9 young (Thomsen 1971) per breeding attempt to reproductive highs in Colorado of 4.4 (Plumpton and Lutz 1994) and 4.9 young (Martin

1973). Geographic variation in climate, the date of nest initiation, prey abundance and availability, and predator community composition likely contribute to regional reproductive differences. Desmond et al. (2000) noted strong annual effects on nesting success of burrowing owls breeding in western Nebraska. Because reproduction can vary dramatically between years, estimates based on one year of data may not be indicative of long-term population trends.

Reproductive output varies with the owls' migratory status. Nest reuse and survival rates are higher in resident burrowing owl populations. The resulting site familiarity may confer reproductive advantages. Although these benefits are expected to diminish in migratory populations (Millsap and Bear 1997), increased reproductive output associated with previous territory experience has been documented in migratory songbirds (Perrins and Smith 1985, Woodard and Murphy 1999). The higher brood sizes reported by Lutz and Plumpton (1999) for migratory females reusing former nest sites suggests the same pattern may hold true for the burrowing owl.

MORTALITY/DISTURBANCE

Mortality differs between resident and migrant burrowing owl populations. Survival rates for resident male and female owls in Florida are 68% and 59%, respectively. Thomsen (1971) reported an adult survival rate of 80% for a resident breeding population in northern California. Available return rate estimates of 47-58% (J. Schmutz, unpublished data), 29-33% (K. DeSmet, unpublished data), and 9% (Pezzolesi 1994) for migratory owls suggest significant over-winter mortality; however, since return rates do not account for between-colony movements across years, reported rates should be considered minimum survival estimates.

Juvenile burrowing owls are particularly susceptible to mortality. Survival to year one is quite low in both resident (Millsap and Bear 1992) and migratory populations (Pezzolesi 1994, O. Dyer, unpublished data). Nestling loss to predators, starvation, or flooding is common during the pre-fledging period, and additional mortality may occur during short-distance dispersal prior to fall migration (Todd 2001). Clayton and Schmutz (1999) observed significant juvenile mortality during the breeding season in Canada. Belthoff et al. (1995), however, reported 77% and 92% survival in pre-fledge and post-fledge (pre-migration) young, respectively; therefore, the majority of juvenile loss may result during migration and on the wintering grounds. Replacement rates and population persistence likelihood depend not only on reproductive capacity and performance, but also on the ability of the population to maintain a sizeable pool of potential breeders. Obtaining detailed data on mortality factors, over-winter survival, and annual recruitment in migratory populations is a priority.

Mammalian predators, particularly badgers, account for most nest predation (Belthoff et al. 1995). Aerial predators and prairie rattlesnakes (*Crotalus viridis*), a common denizen of prairie dog colonies, remain likely sources of additional predation. Burrowing owls frequently line nests with shredded cattle or horse dung (Haug et al. 1993). While the lining may in part serve to insulate the nest cavity, Green and Anthony (1989) noted fewer nest losses at sites lined with livestock manure. Dung may mask the scent of nesting owls and help avoid losses to olfactory-based predators.

Weather can contribute to raptor mortality and reduced reproduction. Exposure can be a source of loss and has been documented in raptors like the Eurasian kestrel (*Falco tinnunculus*) (Village 1986). Sheltered burrows limit burrowing owl exposure;

however, nest failure and mortality from flooding are noted (Desmond et al. 2000, Griebel 2000). The interaction between prey and weather can reduce prey availability to foraging birds, affecting raptor reproductive performance. Precipitation promotes avian starvation by limiting prey availability, reducing foraging efficiency, or causing behavioral tradeoffs between foraging and nest attendance (Murphy 1983, Haug 1985). Reductions in aboveground availability of vertebrate and invertebrate sources during periods of inclement weather may affect owl reproductive performance.

Anthropogenic disturbance may be compensatory or additive to natural mortality in avian populations (Burnham and Anderson 1984). Millsap and Bear (2000) observed a shift in burrowing owl mortality factors with increasing urban development. Increased losses due to human factors in heavily urbanized areas paralleled decreased rates of natural predation. Total mortality was similar across sites along the urban gradient. Additive mortality has been documented in mallards (*Anas platyrhynchos*) (Smith and Reynolds 1992) and willow grouse (*Lagopus lagopus*) (Smith and Willebrand 1999). If regional nesting conditions promote additive mortality, human disturbance may secondarily contribute to burrowing owl population declines.

Mortality owing to human disturbance is reported. Motor vehicle collisions are a source of mortality (Konrad and Gilmer 1984, Haug et al. 1993), and remain a cause for concern as long as owls continue to utilize roadways and roadside perches during foraging activities. Harassment contributed to significant mortality in Florida (Millsap and Bear 2000) and California (Thomsen 1971). Elevated pesticide levels reduced burrowing owl survival in Canada (James and Fox 1987), and promoted egg thinning in breeding populations in California (Gervais et al. 2000). Residual pesticides in prey

populations may contribute to mortality and reduced reproduction (Haug et al. 1993). Shooting has contributed to numerous raptor declines (Gilmer and Stewart 1984, Jacobson and Hodges 1999), and has been diagnosed as a cause of owl mortality in Idaho (Belthoff et al. 1995), Oklahoma (Butts 1973), and South Dakota (G. Schenbeck, personal communication). Disturbance associated with recreational shooting of black-tailed prairie dogs may further reduce population viability by promoting nest desertion and failure. Yet, despite the potential for each factor to affect local mortality and reproductive performance, the magnitude and extent of human activity on burrowing owl population persistence remains unknown (Haug et al. 1993, Holroyd et al. 2001).

CONSERVATION

Habitat loss is a major contributor to wildlife decline and remains a persistent threat to the survival of many species (Huxel and Hastings 1999, Sih et al. 2000). If declining raptor populations are to be effectively conserved, an understanding of what drives reproductive performance and other demographic parameters is necessary. What are the preferred prey types, and how does dietary intake influence demography? What are the primary criteria used in selecting nest sites? And what role does human activity play in reproductive determination? These questions were addressed using a population of burrowing owls breeding on black-tailed prairie dog colonies in the Pawnee National Grassland of northeastern Colorado.

The Pawnee National Grassland was selected as the study site for several reasons. The Pawnee and surrounding portions of Weld County contained the largest statewide burrowing population (VerCauteren et al. 2001); therefore a large pool of potential breeders was available. Burrowing owls occupy the majority of active prairie dog

colonies on National Grasslands (Sidle et al. 2001). In northeastern Colorado, prairie dog colonies provide the majority of suitable habitat and support the highest owl densities; therefore, I expected enough colonies would be occupied on the Pawnee to permit habitat and reproductive comparisons across sites. And finally, public grasslands support grazing, "off-road" vehicle use, and recreational shooting, providing the opportunity to explore the effects of human activity on breeding owls.

In chapter 2, collections of regurgitated castings from active owl nests are analyzed and used to: (1) identify important prey; (2) document temporal and/or spatial shifts in prey use; and (3) relate diet measures to nesting success and productivity data. A multi-scale assessment of nest-site selection follows in chapter 3. Habitat parameters at the individual nest and prairie dog colony scale are recorded, and model selection procedures used to determine the extent to which breeding density and reproductive performance are influenced by nest placement. Chapter 4 addresses recreational shooting of prairie dogs, and explores how shooting activity might affect breeding burrowing owls.

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CHAPTER 2

DIET AND REPRODUCTION IN A COLORADO POPULATION OF BURROWING OWLS

Burrowing owls (*Athene cunicularia*) frequently occupy black-tailed prairie dog (*Cynomys ludovicianus*) colonies where ranges overlap (Desmond et al. 2000). Regional dependence on fossorial rodents for nest sites has resulted in population declines associated with habitat loss and burrowing mammal eradication (Butts 1973). The burrowing owl is currently a listed endangered species in Canada and remains a species of regional concern in the United States (Haug et al. 1993, James and Espie 1997).

Food availability may be limiting burrowing owl reproduction (Green and Anthony 1989, Wellicome 2000); however, few studies provide direct comparison of prey use to reproductive parameters. Burrowing owls utilize a variety of prey types and are described as generalists and seasonal opportunists (Silva et al. 1995, Wiley 1998). Invertebrates are most frequently consumed, however, vertebrate prey have higher moisture content and crude protein levels (Pezzolesi 1994), and typically provide the majority of dietary biomass (Gleason and Craig 1979, Thompson and Anderson 1988).

Preferential use of vertebrate prey may benefit breeding burrowing owls if increased biomass gains translate into larger clutch sizes, healthier, heavier nestlings, and increased survival of adults and young. Use of large vertebrate prey is linked to

increased success in other raptors, including spotted owls (*Strix occidentalis*) (White 1996) and ferruginous hawks (*Buteo regalis*) (Woffinden and Murphy 1977). Numerical and functional responses to small mammal densities in Mediterranean Chile suggest burrowing owls too may benefit from consumption of vertebrate prey (Silva et al. 1995).

Diverse diets may be indicative of low vertebrate abundance. Although Silva et al. (1995) observed increased vertebrate richness in years of mammal abundance, total prey richness declined. Because most richness is derived from invertebrate consumption (Grimm et al. 1985, personal observation), and invertebrate species contribute little to overall prey biomass, nesting pairs with diverse diets may lack the nutrients necessary to be both successful and productive.

Halting regional population declines in burrowing owls requires an understanding of how diet influences demography and, ultimately, population persistence. Effective management of raptors requires management of their prey (Green et al. 1993). Raptor diets are site-specific (Jaksic and Marti 1981); therefore, local studies are needed to identify important prey. Determining how prey density and use affect reproduction is essential, as knowing the relationship between demography and prey is central to developing a conservation strategy (Seamens and Gutierrez 1999).

I report on the relationship between diet and reproduction for burrowing owls breeding in northeastern Colorado. Primary objectives were to (1) describe local prey use and compare results to other studies to address geographic variation in diet; and (2) examine the influence of diet on nesting success and productivity. I expected reproductive output to positively reflect vertebrate use and decrease with increasing diet richness.

STUDY AREA

Breeding burrowing owls were studied on the Pawnee National Grassland, a 78,100-ha mosaic of cultivated, pastoral, and shortgrass steppe located in northeastern Colorado (Fig. 2.1). The climate is typical of mid-continental semi-arid regions. Annual precipitation is 321 mm, falling mainly as rain from April through June (Laeunroth and Sala 1992). Low humidity, high winds, and periodic severe drought characterize the summer breeding season. Mean elevation is 1,650 m, reaching its highest levels at the western boundary. Perennial C_4 grasses are the dominant vegetation, particularly blue grama (*Bouteloua gracilis*) and buffalo grass (*Buchloë dactyloides*). Scarlet globemallow (*Sphaeralcea coccinea*), prickly pear (*Opuntia polycantha*), big sagebrush (*Artemisia tridentata*) and cheatgrass (*Bromus tectorum*) are locally abundant. Moderate grazing by cattle (*Bos taurus*) occurs throughout much of the study area.

METHODS

Monitoring Protocol

Burrowing owl nesting activity was monitored on active black-tailed prairie dog colonies from 9 May through 12 August 2000. Colorado Division of Wildlife and U.S. Forest Service personnel provided prairie dog colony locations. Three, one-hour surveys confirmed owl presence/absence at each site. On occupied colonies, potential nests were identified using preliminary observations of mated pairs; ground inspection of burrows for the presence of shredded dung, castings, and whitewash at the burrow entrance assisted in nest identification. Nest sites were staked with 46-cm garden stakes placed 3 m north of the burrow entrance to facilitate mapping and identification, and monitored weekly. Continued observation of a mated pair, or the presence of eggshell fragments

and nesting-related behaviors (ex. mate feeding) confirmed breeding status. Successful nests raised one or more young to fledging age (28 days; Zarn 1974). The maximum number of post-fledging young observed at the nest entrance denoted minimum productivity. Photographic keys aided in age determination of young (Priest 1997).

Prey Identification

Fresh castings were collected at nest sites every 2 weeks from 25 May to 27 July 2000. Castings were identified by the date, nest, and prairie dog colony of collection, and stored in sealed plastic bags prior to analysis. Coloration and the presence/absence of moisture assisted in sample aging. I recorded casting dry weight and soaked castings overnight in an 8% NaOH solution to remove hair and other digestible materials (Degn 1978). Vertebrate and arthropod remains were separated, identified to the lowest taxonomic level possible (usually genus or species), and the number of individuals counted. Diagnostic keys and reference collections maintained by the Colorado State University Department of Entomology and the Denver Museum of Nature and Science aided in prey identification. Minimum individual counts reflected the number of single or paired anatomical features present in castings (Silva et al. 1995). Vertebrate prey remains may be spread across several pellets, creating the possibility of overestimation (Plumpton and Lutz 1993); therefore, I followed the methodology of Schmutz et al. (1991) to achieve conservative vertebrate counts.

Several diet measures were recorded to document prey use and examine the relationship between diet and reproduction. For descriptive purposes, prey use was expressed as both a relative frequency of the total individuals in the diet and a relative occurrence in castings. In reproductive analyses, I measured two nest-level diet

parameters: vertebrate prey use and diet richness. Vertebrate use was a proportional measure of casting vertebrate content. Diet richness represented a minimum estimate of prey diversity. Because prey remains were consistently identified to family, I used the number of prey families present in castings as a richness index. Casting measures subsequently were averaged by nest prior to reproductive analyses. Vegetation, seed, and rock counts were included in frequency and occurrence estimates but excluded from reproductive analyses, as they likely resulted from incidental ingestion.

A review of the burrowing owl diet literature provided the basis for evaluating geographic variation in prey use. For each study, I recorded the ratio of invertebrate to vertebrate prey, and the three most frequently consumed prey families. Additionally, prey diversity was noted when possible to address diet site-specificity and uniqueness.

Statistical Analyses

Mixed model analysis of variance (ANOVA) assessed temporal variation in diet measures. Vertebrate prey use and diet richness served as response variables. Sampling date was the primary explanatory variable. A random prairie dog colony effect was included in models to account for potential variation in diet among breeding sites. I considered prairie dog colony a random effect, as sampled sites represented a subset of the total breeding population on the Pawnee National Grassland. Chi-square comparison of residual log-likelihood values between the full model and the model with the random effect tested the significance of prairie dog colony. Significant effects were included in models where appropriate. I assigned sampling dates numeric values: 1 represented 1 May 2000, 32 represented 1 June 2000, and so on. Log and square-root transformation corrected for non-normality in respective diet measures.

Reproductive performance was monitored at a total of 103 nests during the 2000 breeding season. To eliminate statistical bias associated with the inclusion of late season successful pairs (Lehman et al. 1998), I backdated young to determine hatch date and excluded from analyses all nests located post-hatch ($n = 3$). Failed nests with no emergent young were excluded if nest identification occurred after the median hatch date.

A logistic regression modeled the binomial response measure, nesting success. Productivity was assessed by mixed model ANOVA. Explanatory variables in reproductive models included vertebrate prey use and diet richness. As the breeding cycle from egg laying to fledging remained the primary interest, I excluded diet data collected post-fledging and based analyses on nests for which a minimum of one casting was collected ($n = 59$).

Normality assumptions were tested for response and predictor variables using the Shapiro-Wilk statistic (PROC UNIVARIATE, SAS Institute 2000). Log (vertebrate prey use) or square root transformation (diet richness, productivity) corrected for data non-normality. Influential data and outliers were identified and eliminated if residual plots indicated exclusion significantly improved model fit. I tested for collinearity of explanatory variables, and retained model variables with Pearson correlation coefficients < 0.7 ($P > 0.05$). All analyses were conducted using SAS v. 8.1 (SAS Institute 2000). Significance was held at the $P < 0.05$ level. Reported values are presented as means ± SE unless otherwise noted.

RESULTS

Prey Use

Casting analysis revealed a diverse diet. Burrowing owls utilized a minimum of 84 prey species from 26 families and 9 orders. Castings (weight: $\bar{x} = 2.2$ g, SE = 0.2 g, n

= 116) contained on average 21.0 ± 1.3 individuals. Invertebrates were more frequent than vertebrates across all samples (Table 2.1; Appendix A). Insect families Scarabaeidae, Carabidae, and Gryllacrididae accounted for ca. 57% of the individuals recovered. The ground beetle *Pasimachus elongatus* (Family: Carabidae) was prevalent in the diet, occurring in approximately two-thirds of castings. Vertebrate prey were far less common (Table 2.1). Burrowing owl diets contained 11 vertebrate species (Appendix B); northern pocket gophers (*Thomomys talpoides*), thirteen-lined ground squirrels (*Spermophilus tridecemlineatus*), deer mice (*Peromyscus maniculatus*), prairie voles (*Microtus ochrogaster*), northern grasshopper mice (*Onychomys leucogaster*), and lark buntings (*Calomospiza melanocorys*) being the most abundant. And while invertebrate prey occurred in all castings, fewer than half of castings (49%) contained vertebrate remains.

Vertebrate consumption varied with sampling date ($F_{1,54} = 6.70$, $P = 0.01$; Fig. 2.1). Although vertebrate prey comprised only 4% of casting remains (vegetation counts excluded) and never exceeded 29% for any given casting, owls consumed vertebrates at levels sufficient to detect dietary shifts in prey use. Diet richness did not vary with sampling date ($F_{1,113} = 0.01$, $P > 0.9$). No colony effect was evident for either vertebrate use or diet richness (all $P > 0.3$).

Diet Effects

Seventy-seven nests successfully fledged young in 2000. Mean productivity was 3.6 ± 0.3 young per breeding attempt (range = 0 – 9, $n = 100$) and 4.7 ± 0.2 young per successful nest. Median hatch date was 7 June. Colony location affected fledging rates ($\chi^2_1 = 12.5$, $P < 0.001$). I attributed site effects on reproductive performance to extensive

Table 2.1. Frequency and occurrence of prey items in burrowing owl castings (n = 116) at the Pawnee National Grassland, 2000.

Prey items	Frequency (%)	Occurrence (%)	Total individuals
INVERTEBRATES	*93.14*	*100.00*	*2358*
ARACHNIDA			
Araneae			
Salticidae	0.59	11.21	15
Solifugae			
Eremobatidae	1.14	20.69	29
INSECTA			
Coleoptera			
Carabidae	20.38	83.62	516
Cerambycidae	7.31	46.55	185
Chrysomelidae	0.12	2.59	3
Cicindelidae	0.51	11.21	13
Curculionidae	1.46	9.48	37
Histeridae	0.16	0.86	4
Hydrophilidae	0.04	0.86	1
Scarabaeidae	29.23	84.48	740
Silphidae	3.59	46.55	91
Tenebrionidae	6.64	51.72	168
Unknown	0.16	0.86	4
Hymenoptera			
Formicidae	3.24	12.07	82
Halictidae	0.12	2.59	3
Ichneumonidae	0.24	2.59	6
Orthoptera			
Acrididae	4.82	37.93	122
Gryllacrididae	7.86	46.55	199
Gryllidae	5.17	37.93	131
MALACOSTRACA			
Decapoda			
Cambaridae	0.36	7.76	9
VERTEBRATES	*3.02*	*49.14*	*76*
AVES			
Passeriformes			
Alaudidae	0.28	4.31	7
Fringillidae	0.28	6.03	7
Unknown	0.20	4.31	5
MAMMALIA			
Rodentia			
Cricetidae	0.99	18.97	25
Geomyidae	0.67	13.79	17

Heteromyidae	0.08	1.72	2
Sciuridae	0.36	7.76	9
Unknown	0.12	2.59	3
REPTILIA			
Squamata			
Phrynosomatidae	0.04	0.86	1
OTHER	*3.87*	*23.28*	*98*
Vegetation	1.38	18.10	35
Seeds	0.04	0.86	1
Rocks	2.29	15.52	58
Unknown	0.16	3.45	4
TOTALS	100.03		2532

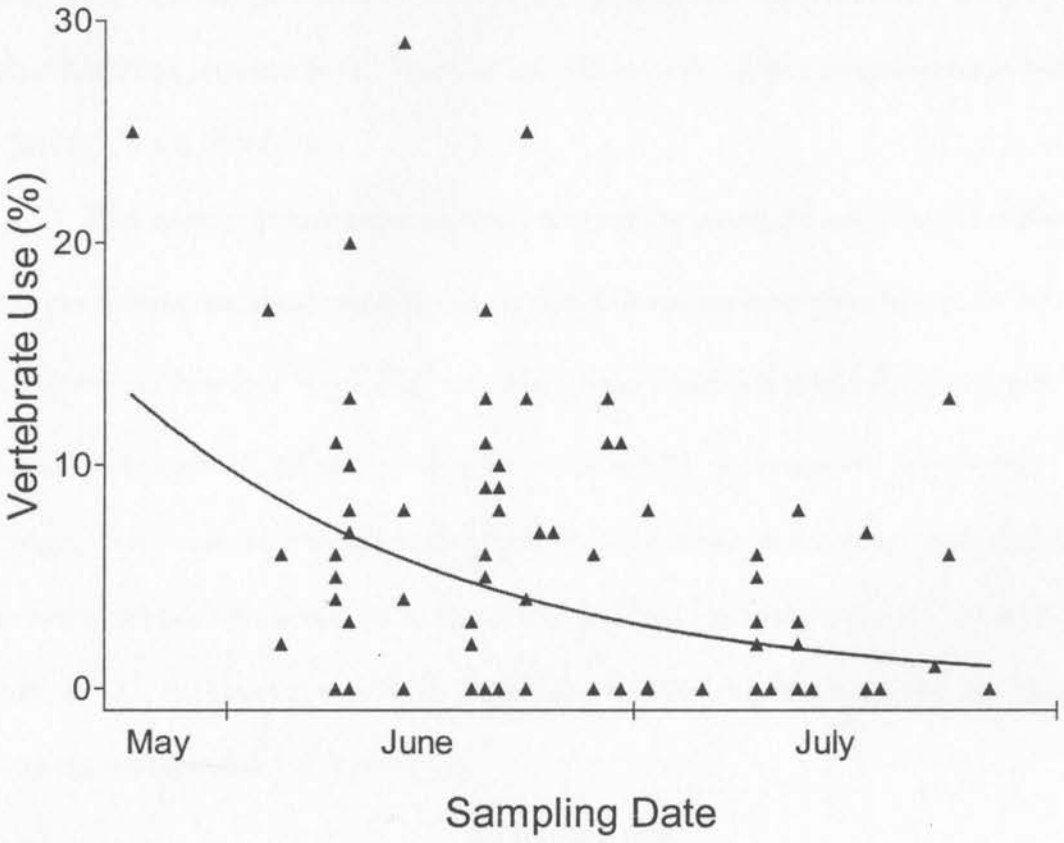

Figure 2.1. Relationship between the percent of vertebrate individuals represented in burrowing owl castings (n = 115) and sampling date, 2000.

nest failure and low productivity at three eastern colonies. Log-likelihood reanalysis after excluding the data for the colonies in question yielded a non-significant colony effect ($\chi^2_1 = 0.8$, $P > 0.3$).

Diet weakly influenced measured reproductive parameters (Table 2.2). Nesting success showed marginal declines with increasing diet richness (successful: $\bar{x} = 5.5$, SE = 0.3, $n = 52$; failed: $\bar{x} = 7.3$, SE = 1.1, $n = 7$) and vertebrate prey use (successful: $\bar{x} = 5.5$, SE = 0.9, $n = 52$; failed: $\bar{x} = 9.1$, SE = 2.3, $n = 7$). Although not significant, fledging rates showed similar trends (Table 2.2). Diet had no effect on productivity measures when only successful nests were considered (vertebrate use: $F_{1,29} = 0.63$, $P = 0.44$, $n = 32$; richness: $F_{1,29} = 0.04$, $P = 0.84$, $n = 32$). Vertebrate use and diet richness were not correlated ($r = 0.1$, $P > 0.5$).

DISCUSSION

Prey Use

Burrowing owls foraged opportunistically, using invertebrates to supplement consumption of more profitable vertebrate prey. Frequent use of invertebrate prey was a theme common to all diet studies. Despite differences in species composition, invertebrates remained the predominant prey type used (Table 2.3). A lack of adequate vertebrate sources and the ready availability of invertebrate prey may have contributed to their widespread use by foraging owls.

The structure and composition of shortgrass prairie vegetation limited vertebrate abundance and availability (Stapp 1996), and consequently their intake. Numerical and functional responses to small mammal population fluctuations in Chile (Silva et al. 1995), and the owls' opportunistic use of vertebrate sources where regionally abundant

Table 2.2. Fixed effects for models comparing burrowing owl nesting success and productivity to measured diet parameters.

	Nesting Success			Productivity		
Source	χ^2	df	*P*	*F*	df	*P*
Diet richness[a]	3.59	1	0.06	2.12	35	0.15
Vertebrate use[b]	3.22	1	0.07	2.09	35	0.16

[a] Results based on square-root transformed data.

[b] Results based on log-transformed data.

Table 2.3. Invertebrate:vertebrate (I:V) composition and important prey in diet studies of the burrowing owl.

Study	Location	I:V	Dominant Plant Community	Most Frequent Prey Taxa[a]
This study	Colorado	93:3	Shortgrass Prairie	Scarab., Carab., Grylla.
Brown et al. (1986)	Oregon	74:14	Shrubsteppe	Acrid., Scarab., Stenop.
Gleason & Craig (1979)	Idaho	91:9	Shrubsteppe	Grylla., Solpu., Silph.
Green et al. (1993)[b]	Oregon	92:8	Shrubsteppe	Teneb., Scarab., Grylla.
Green et al. (1993)[b]	Washington	83:17	Shrubsteppe	Teneb., Scarab., Hetero.
Grimm (1985)	Washington	81:19	Right-of-Ways/Canal Banks	Carab., Teneb., Acrid.
MacCracken et al. (1985)	S. Dakota	57:24[c]	Shortgrass Prairie	Carab., Teneb., Hister.
Marti (1974)	Colorado	92:8	Shortgrass Prairie	Carab., Grylli., Scarab.
Plumpton & Lutz (1993)	Colorado	56:33	Shortgrass Prairie/Cheatgrass	Cricet., Teneb., Silph.
Schlatter et al. (1980)	Chile	79:21	—	—
Silva et al. (1995)	Chile	87:13[d]	Thorn Scrub/Forest	Teneb., Scorp., Cricet.
Thompson & Anderson (1988)	Wyoming	95:5	Shortgrass Prairie	Acrid., Carab., Formic.
Wiley (1998)	Dom. Republic	53:47	Acacia-Cactus Dry Woodland	—

[a] Top prey families based on frequency of individuals in diet. Families include: Acrididae, Carabidae, Cricetidae, Formicidae, Gryllacrididae, Gryllidae, Heteromyidae, Histeridae, Scarabaeidae, Scorpionidae, Solpugidae, Stenopelmatidae, Tenebrionidae

[b] Data taken from same study.

[c] Results based on data pooled from May-August 1981.

[d] Results based on 1990-1992 breeding season data only.

(Plumpton and Lutz 1993, Wiley 1998; Table 2.3) suggest vertebrates remain the preferred prey of foraging owls. Low vegetation height and increased bare ground characteristic of shortgrass steppe habitat, and the general lack of quality seed by the dominant plant species, buffalo grass and blue grama, offer little in the way of protective cover and forage for small mammals. As a consequence, densities of preferred prey, particularly rodents, were low relative to other grassland habitats. Even in areas where abundant vertebrate sources were to be found, availability may have been limited. Cultivated lands, road right-of-ways, and irrigation ditches supported greater small mammal abundances (Bechard 1982, P. Stapp, unpublished data); however, the high density and vertical structure of cropland vegetation in early summer can reduce the profitability of such prey "hotspots" to breeding raptors (Bechard 1982).

Compounding this problem is the tendency for vertebrate consumption to diminish through the breeding season. Declines in vertebrate use are well documented and may reflect decreasing abundance of preferred prey (Marti 1974, MacCracken et al. 1985). Lacking an adequate vertebrate base, and faced with dwindling prospects, owls may be forced to seek out alternate prey to supplement vertebrate intake and meet short-term (daily) requirements. This combination of factors may explain low vertebrate use across shortgrass habitat studies (Table 2.3).

Invertebrates, being both abundant and available, provided nesting owls with an attractive alternate food source. Many invertebrate families, particularly beetles, were commonly observed in pitfall traps (Hoffman 2000), and consistently occurred at higher densities than small mammals (P. Stapp, unpublished data). Invertebrates were also highly visible. The low vertical structure and density of shortgrass vegetation enhanced

prey detection, increasing prey susceptibility to foraging owls. Casting analyses suggested owls used highly visible families, such as Carabaeidae, Scarabaeidae, and Tenebrionidae in proportion to their abundance.

The burrowing owls' use of habitats containing abundant invertebrate prey and the presence of diurnal foraging contributed to invertebrate consumption. Most foraging (95%) occurs within a 600-m radius of the nest site (Haug and Oliphant 1990), encompassing much of the prairie dog colony itself. Within prairie dog habitat, invertebrate groups do not differ in abundance from that of adjacent shortgrass habitat (J. Junell, unpublished data). Vertebrate densities are lower on prairie dog colonies (P. Stapp, unpublished data), thus owls are more likely to encounter invertebrate prey. Scarabs and other beetles occasionally occupy the burrow systems of vertebrate species (Borror et al. 1989). Burrowing owls may cue in on accessible invertebrate sources in and around the nest mound (Schlatter et al. 1980, Green et al. 1993), furthering promoting invertebrate intake. Crepuscular foraging is most common, but short, diurnal foraging trips are reported (Thomsen 1971, Haug et al. 1993). Only invertebrate species are targeted during the day (Marti 1974, Plumpton 1992); therefore, the owls' capacity for acquiring invertebrate prey does not incur the same time limitations that accompany vertebrate prey use.

Spatial variation in vegetation, weather, and natural and anthropogenic features provided nesting owls on the Pawnee National Grassland with unique subsets of potential prey. Burrowing owls responded to these spatially dependent invertebrate sources when and where available. Pairs nesting on colonies adjacent to permanent pools had high levels of crayfish (*Cambarus* sp.) in casting remains; at no other nests were such prey

found. Similarly, the lone giant water scavenger beetle (*Hydrophilus triangularis*) occurred in the casting of an owl nesting in close proximity to a water tank.

Invertebrate consumption may benefit breeding burrowing owls and their young. Inclement weather during the summer season limits prey availability (Murphy 1983), reduces foraging efficiency (Murphy 1983, Village 1986), and can lead to lower rates of nesting success and survival in raptor populations (Steenhof et al. 1997, Chapter 3). Having a constant, albeit reduced, food source may allow owls to obtain minimal nutrient levels necessary to survive these short-term adverse conditions. The proximity of invertebrate sources to the nest may also benefit owls by increasing nest attendance. Predation is a primary source of avian nest failure (Martin 1993). Being able to acquire nutrients within the immediate nest vicinity may allow owls to devote more time to nest guarding, reducing instances of depredation. Young owls frequently acquire foraging skills by "attacking" small invertebrates at the nest site. While invertebrate prey do not provide significant biomass gains, their use as an instructional tool may provide skills critical to future breeding success.

Diet Effects

Reproductive performance was weakly influenced by diet. Low vertebrate availability may explain the lack of a positive association between reproduction and vertebrate use in this study. Vertebrate prey provide the majority of dietary biomass for breeding burrowing owls (Gleason and Craig 1979, Wiley 1998), and higher productivity at elevated levels of vertebrates consumption is reported (Plumpton and Lutz 1994). Despite low vertebrate use on the Pawnee National Grassland, reproductive rates did not differ from those of owls breeding in other prairie dog habitat (Butts 1973, Griebel 2000).

Vertebrate consumption may have met minimum dietary levels necessary to initiate nesting, but may not have been sufficient to benefit breeding owls through increased biomass gains (Smith et al. 1981). Although invertebrates provide little biomass, their use at regular intervals and during periods of inclement weather may serve as a buffer against reproductive losses associated with declines in preferred prey. Contrary to expectations, nesting success showed a marginal decline with increasing vertebrate prey use. Nest failure induced by localized rainstorms and small sample size at failed nests (n = 7) may explain this negative trend (Table 2.2).

Studies suggest owls rely on fewer prey taxa under good conditions when vertebrate sources are abundant (Grimm et al. 1985, Silva et al. 1995). Although not significant, the tendency for nesting success to increase with decreasing diet richness supports this idea. Diversity was primarily a function of invertebrate prey use (73 of 84 species identified). When owls lacked the vertebrate prey necessary to achieve significant biomass gains, owls consumed more invertebrate species but tended towards lower success and fewer young.

MANAGEMENT IMPLICATIONS

Continued success of generalist raptor species may ultimately depend on their ability to utilize a diverse prey base (Karpanty and Goodman 1999). For burrowing owls of the shortgrass steppe, managing vertebrate populations will help sustain minimum prey levels necessary for successful nesting. Incorporating invertebrate prey into management plans also will be essential. Invertebrates provide a readily available food source and may help owls avoid short-term food shortages. Activities that adversely affect the abundance and availability of families Carabidae, Scarabaeidae, Gryllacrididae and other

large invertebrate prey should be identified and minimized during the breeding season. Determining the effect of prairie dog flea powder on prey sources within the burrow system will be of particular importance.

Burrowing owls prefer to nest in active prairie dog colonies (Butts 1973, Hughes 1993), and occupy the majority of such sites on the Pawnee National Grassland. Maintaining an abundance of widely dispersed colonies will mitigate against the effects of spatial variation in prey availability and weather conditions, making it less likely that annual fluctuations in reproduction threaten population persistence.

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CHAPTER 3

A MULTI-SCALE ASSESSMENT OF THE REPRODUCTIVE CONSEQUENCES OF NEST PLACEMENT IN BURROWING OWLS

Nest placement may be the product of factors operating at multiple scales of resolution. At a coarse scale, suitable habitat and matrix are distinguished, establishing the abundance and distribution of potential nesting habitat. Within suitable habitat, differences in biotic and abiotic conditions create patches of varying quality. Characteristics of the nest (orientation, microclimate), the nest vicinity (perch availability, predator/prey abundance and availability, location and density of competitors), or the surrounding landscape (connectivity, habitat composition and configuration) may determine whether a site becomes occupied, and if so, its reproductive potential. Selection may proceed in a step-wise fashion of decreasing scale (i.e. landscape → nest) with the importance of habitat features being scale-dependent. Preferences at larger scales would determine the variability of habitat parameters operating at finer scales, and consequently their range of influence on demographic measures. Conversely, selection may occur in a hierarchical fashion, independent of scale, and based on rankings of parameter importance to some fitness measure(s). In this latter scenario, importance is selection-dependent. Studies conducted at a single scale of resolution may fail to explain a significant portion of variation if the wrong scale is

chosen, regardless of the selection method employed. Single-scale studies may also contribute to overestimation of parameter importance if overriding habitat measures are ignored. By avoiding such problems, multi-scale analyses provide a framework for understanding complex nesting patterns that involve decisions at multiple spatial scales. Implicit in this multi-scale framework is a need for detailed review of species' life history in order to understand breeding requirements and identify parameters of potential importance.

For the burrowing owl (*Athene cunicularia*), a ground-nesting raptor of special concern in the western U.S. (James and Espie 1997), nest selection is a multi-step process. Although capable of nest excavation (Thomsen 1971, Millsap and Bear 2000), high breeding densities in areas of fossorial rodent activity suggest regional dependence on rodent populations for nest sites. In the North American Great Plains, burrowing owl use of black-tailed prairie dog colonies (*Cynomys ludovicianus*) is common (Desmond 1991). The abundance and location of prairie dog habitat determines the spatial arrangement and extent of suitable breeding habitat. Within this spatial complex of prairie dog habitat, burrowing owls must select a colony and nest in which to breed.

The net loss, degradation, and fragmentation of prairie dog habitat, coupled with eradication through poisoning and sylvatic plague (*Yersinia pestis*), have contributed to a >98% reduction in prairie dog numbers (Miller 1994). While prairie dog population declines have limited nesting and foraging opportunities (Bent 1938, Butts 1973, Warnock 1997), owls do not use remaining prairie dog colonies equally. Although occupation rates may be quite high, avoidance of otherwise seemingly suitable habitat suggests a proclivity for select colony attributes (Plumpton and Lutz 1993). Active

colonies are more frequently occupied by burrowing owls (Sidle et al. 2001). Increasing vegetation height and decreasing burrow stability limit the attractiveness of inactive sites; colonies typically fall into disuse within 1-3 years after becoming inactive (Butts 1973). Large colonies tend to support more owls (Toombs 1997, Ekstein 1999, Desmond et al. 2000), and may confer higher nesting success (Desmond et al. 2000). Coulombe (1971) suggested burrow availability as a limiting factor to burrowing owls. Areas of high burrow density may provide additional breeding opportunities and a greater range of nest sites from which to choose. Although a large prairie dog population may limit the number of burrows available to nesting owls, prairie dog activity may reduce nest depredation by providing alternate prey or by alerting owls to nearby predators (Desmond et al. 2000). Use of high burrow density habitat (Plumpton and Lutz 1993, Ekstein 1999) and areas of increased prairie dog activity (Hughes 1993) are reported.

The burrow provides a sheltered breeding environment and serves as a refuge from aerial predators and adverse weather. Burrows in short, sparse vegetation are preferred, presumably because the increased horizontal visibility conferred enhances detection of predators and prey in the nest vicinity (MacCracken et al. 1985, Green and Anthony 1989). Knowles et al. (1982) observed a similar preference for short vegetation in mountain plovers (*Charadrius montanus*), another associate of the prairie dog. In addition to the physical attributes at or near the nest, the spatial distribution of burrows and other nesting pairs may influence final nest placement. Breeding pairs and their young use a number of supplemental "satellite" burrows during the breeding cycle. These satellite mounds may provide critical refuge from adverse weather or predators (Henny and Blus 1981). If satellite availability reduces predation risk, reproductive

losses should decrease as more burrows are made available to nesting pairs. Desmond et al. (2000) reported increased nest success in high satellite burrow density habitat. Owls nesting in close proximity may incur competitive costs if resources are limiting. Nearest-neighbor distance was important to owls using badger (*Taxidea taxus*) burrows in Idaho (Green and Anthony 1989), and Griebel (2000) suggests the same may hold true for owls nesting in prairie dog colonies.

Protecting and sustaining viable populations of declining raptor species requires an understanding of: (1) the habitat features that drive nesting patterns and the scale at which they operate; and (2) the reproductive consequences of nest placement. Identifying prime breeding habitat will be an important step in prioritizing conservation goals and allocating limited resources to meet management objectives. Relating habitat data to fitness measures is also important. Occupancy rates, the number of nesting pairs, and nesting density have been the primary response variables of interest; few burrowing owl studies have examined reproductive performance and variation among occupied sites. Because use of a habitat is not always an appropriate indicator of its quality (Van Horne 1983), reliance on density or nest estimates alone may yield misleading conclusions. Supplementing such information with reproductive, survival, or recruitment data will provide a clearer picture of overall breeding conditions and equip management with the best recommendations for effective conservation.

Here, I report on nest-site selection and reproductive performance of burrowing owls breeding on black-tailed prairie dog colonies in the Pawnee National Grassland, Colorado. The primary objective of this study was to model nest and colony attributes to determine the scale and extent to which breeding density and reproductive output were

affected by measured habitat parameters. At the nest level, we used satellite burrow density and neighbor distance as surrogates of predation risk and intraspecific competition to determine the extent to which reproduction might be affected by biotic interactions.

STUDY AREA

Fieldwork was conducted on black-tailed prairie dog colonies located in the shortgrass steppe of Weld County, Colorado. Weld County contained the largest statewide burrowing owl population and ranked second in the amount of available prairie dog habitat in 1999 (VerCauteren et al. 2001). Although public and private lands throughout the county supported breeding owls, most fieldwork occurred on public lands within the Pawnee National Grassland (hereafter Pawnee). Encompassing 78,100 ha of native shortgrass prairie, rangeland, and dry and irrigated cropland, the Pawnee has a climate typical of mid-continental semi-arid regions. Precipitation averages 321mm, the majority occurring as rain from May to September. Low humidity, high winds, and severe drought are common in the summer. Vegetation is characteristic of shrubsteppe habitat. Blue grama (*Bouteloua gracilis*) is the dominant species (Lauenroth et al. 1987); buffalo grass (*Buchloë dactyloides*) is also abundant. Moderate grazing by cattle (*Bos taurus*) occurs throughout the study area.

METHODS

Reproductive Determination

Breeding burrowing owls were monitored from 17 April through 3 August 1999 and from 9 May through 12 August 2000. The Colorado Division of Wildlife (J. Wagner, personal communication) and U.S. Forest Service (Ball 1998) provided locations of

prairie dog colonies occupied by burrowing owls. Occupied sites were located in the western and southeastern portions of the Pawnee. The northeast region lacked burrowing owls, presumably due to an absence of nest-providing species.

Burrowing owl breeding sites were identified during preliminary surveys of occupied colonies ($n = 25$). Surveys consisted of repeated scans with a spotting scope (15-60×) from a vehicle or blind. Observations were made during early morning (0600-1000) and late afternoon (1500-1900), periods of peak owl activity, and were timed to coincide with nest establishment (April-May). Identification of territorial pairs was followed by ground inspection of burrows within core use areas to confirm nesting; the presence of shredded dung, prey castings, and whitewash characterized active sites. I placed wooden stakes 3 m north of the burrow entrance for monitoring purposes, and visited nests weekly to determine reproductive output. I deemed nests successful if one or more young reached a fledging age of 28 days (Zarn 1974). Minimum productivity was expressed as the maximum number of post-fledging young observed at the nest entrance. Photographic keys aided in age determination of young (Priest 1997). Pairs identified late in the breeding season tend to be more successful (Lehman et al. 1998). I backdated young to determine hatch date and excluded from analyses nests located after the incubation period.

Habitat Measures

Geographic locations of burrowing owl nest sites were captured using a Global Positioning System (GPS) unit. Mapping nests in late fall after all young had fledged ensured minimal disturbance to breeding pairs. The distance between nearest-nesting conspecifics was calculated by entering GPS data into ArcInfo (ESRI 1997), a

Geographic Information Systems (GIS). Nest sites had to be active during the same time period to qualify for nearest-neighbor analyses. I also estimated satellite burrow availability at occupied nests. At each nest mound, I used a measured rope to record the number of satellite mounds within a 30-m radius of the nest entrance. Preliminary surveys suggested a minimum burrow entrance size for satellite occupation, and a general avoidance of unstable mounds. All burrows were counted provided (1) the diameter of the burrow entrance was > 8 cm, and (2) the burrow was not degraded or filled in with litter. I did not distinguish between burrows actively occupied by prairie dogs and those unoccupied, as owls used both types on occasion (Appendix C, D).

Prairie dog colonies were mapped with a GPS receiver in May-June of 1999 and 2000; the outermost active burrows delineated colony boundaries. Size of prairie dog colonies was obtained by entering the habitat data into the GIS database. I modified the burrow count protocol of Biggins et al. (1993) to estimate inactive and active prairie dog burrow densities. Using colony size estimates obtained from the GIS, I calculated the number of 30-m radius circular plots necessary to sample 5% of each colony. Results from Biggins et al. (1993) suggest this sampling scheme is sufficient to achieve accurate density counts. Plots were randomly placed across colonies provided they did not intersect colony boundaries or one another. Active and inactive burrow counts were recorded for individual plots. Observation of a prairie dog, the presence of fresh scat, and signs of recent burrow modification distinguished active burrows (Desmond and Savidge 1996). Webbed or degraded burrows were excluded from count estimates. Plot counts were averaged by colony and expressed on a per hectare basis (Appendix E). Due to time constraints, active and inactive burrow densities were estimated for 2000 only.

Statistical Analyses

I constructed a suite of models to examine the influence of habitat on demographic measures at the burrowing owl nest and prairie dog colony levels. Each model series consisted of a global model containing all parameters of interest, and a subset of models containing one or more global model predictors (Table 3.1). Candidate models were developed *a priori* based on a review of the burrowing owl literature. I used logistic regression to examine the influence of satellite burrow density and nearest-neighbor distance on nest success. Preliminary observations suggested a strong annual effect; therefore, year was included in the global model and several submodels. Nest productivity models were generated by generalized linear model analysis (PROC GENMOD; SAS Institute 2000). I modeled data after a Poisson distribution because nest counts yielded zero young on more than one occasion. Model predictors included those used in nest success analyses. At the colony scale, I tested for effects of colony size, active burrow density, and inactive burrow density. Response measures in colony analyses included: nest density, nesting success (successful nests/total nests), and productivity (mean young fledged/nest). I used multiple regression to develop models for predicting breeding densities of burrowing owls. Logistic and linear regression modeled nesting success and productivity data, respectively. Productivity estimates were weighted to adjust for disproportionate nest numbers among occupied colonies. Because burrow density data were lacking for 1999, no year effect was included in colony-based models. Instead, I used a repeated measures analysis of variance (ANOVA) to test for demographic trends between years. I considered the repeated analysis appropriate because response measures were taken from the same colonies in both years.

Table 3.1. Habitat models used to predict burrowing owl breeding densities and reproductive performance on the Pawnee National Grassland.

	Nest Scale	Colony Scale
Model [a]	Parameters [b]	Parameter [c]
GB	year, neighbor, satellite	size, iburrows, aburrows
C1	neighbor	size, iburrows
C2	satellite	size, aburrows
C3	neighbor, satellite	iburrows, aburrows
C4	year	size
C5	year, neighbor	iburrows
C6	year, satellite	aburrows

[a] GB = global model; C = candidate model.

[b] Year, nearest-neighbor distance (m), and satellite burrow density (30-m radius).

[c] Colony size, density of inactive burrows (/ha), and density of active burrows (/ha).

Candidate models from linear and logistic analyses were evaluated using Akaike's Information Criterion (AIC: Akaike 1973). This information-theoretic approach avoids many of the shortcomings of traditional hypothesis testing (e.g., selection of an arbitrary α level that may be of questionable biological significance, reliance on significance testing for parameter inclusion; Anderson et al. 2000, Roberson 2000). Model likelihood is assessed based on the data and the set of candidate models. Lower AIC scores (i.e. higher Akaike weights (w_i)) are indicative of better models (Burnham and Anderson 1998). In each series of models, I scaled results to estimate relative differences in AIC values (best model: Δ_i AIC = 0.0). Scores that differed by <2 were indicative of competing models (P. Kennedy, personal communication). I summed w_i for all models containing the habitat parameter of interest. Comparison of summed weights to one another and the best model provided a relative index of parameter importance (Burnham and Anderson 1998). Equal representation of parameters across models ensured balance in importance analyses. Likelihood ratio tests and chi-square analyses supported model comparisons (see Murphy 2001: 1307). A small-sample correction of AIC (AIC_c: Hurvich and Tsai 1989) adjusted for low sample size in colony-based models.

Response and predictor variables were tested for normality using Shapiro-Wilk statistics and residual plots (PROC UNIVARIATE; SAS Institute 2000). Log or square root transformation corrected for data non-normality. I tested for collinearity of explanatory variables, and retained model variables with Pearson correlation coefficients < 0.7 ($P > 0.05$). All analyses were conducted using SAS v. 8.1 (SAS Institute 2000). Significance was held at the $P = 0.05$ level. Reported values are presented as means ± SE unless otherwise noted.

RESULTS

Demography

One hundred-forty breeding pairs (71%) were successful, fledging on average 3.7 ± 0.2 young per nest. Mean productivity for all breeding attempts was 2.6 ± 0.2 young (range = 0-9, n = 197). Median hatch date in 2000 was 7 June (n = 100), approximately two weeks earlier than the median hatch date in 1999 (n = 97). Reuse of prairie dog colonies was common. Of the 23 colonies occupied by breeding owls in 1999, 91% supported nests in 2000; exceptions were a colony subjected to poisoning and a colony extirpated by plague, both in late 1999.

Nest Scale

Nearest-neighbor distance and satellite burrow density were poor predictors of reproductive performance. The top model for nesting success included year (β = -0.26, CI = -0.58, 0.06) but neither habitat measure (Table 3.2). The w_i of the top model was nearly twice that of the next best model; however, the two models did not differ statistically (χ^2_1 = 1.15, P = 0.28). Pairs nesting in 2000 had a marginally higher rate of success (77%) compared to pairs nesting in 1999 (65%). The low R^2 of the global model indicated a poor fit of model parameters to nesting success data (Table 3.2).

Akaike weights indicated the top productivity model did not differ from those included in the 95% confidence set; however, all competing models included a year effect (Table 3.2). In contrast, no habitat-based model had a w_i >0.00 when year was ignored. The relative weight of evidence for year was greater than that of either habitat measure and that of the best model, suggesting an annual effect on productivity (Table 3.3). Nests in 2000 fledged more young per breeding attempt than did their 1999 counterparts ($F_{1,20}$ = 17.77, P < 0.001; Fig. 3.1).

Table 3.2. Habitat models (95% confidence sets) used to predict burrowing owl nest performance on the Pawnee National Grassland, 1999-2000. Models presented in order by relative strength of Akaike weights (w_i). R^2 values given for global models and best models as identified by AIC selection.

Demographic Parameter	Model	*n*	K	R^2	AIC_c	ΔAIC_c	w_i
Nest Success	year	189	3	1.3	227.74	0.00	0.35
	year, neighbor	189	4		228.89	1.15	0.20
	year, satellite	189	4		229.71	1.97	0.13
	neighbor	189	3		230.09	2.35	0.11
	satellite	189	3		230.23	2.49	0.10
	year, neighbor, satellite	189	5	1.8	230.88	3.14	0.07
Productivity	year	189	3		-14.07	0.00	0.32
	year, neighbor	189	4		-13.93	0.14	0.29
	year, satellite	189	4		-13.27	0.80	0.21
	year, neighbor, satellite	189	5		-12.93	1.14	0.18

Table 3.3. Relative importance of nest-level habitat variables to burrowing owl reproductive performance in northeastern Colorado, 1999-2000. Importance values were calculated by summing Akaike weights (w_i) for all models containing the habitat parameter of interest.

Response Measure	Nearest-Neighbor distance (m)	Satellite Burrow density (30-m radius)	Year
Nest Success	0.42	0.35	0.75
Productivity	0.47	0.39	1.00

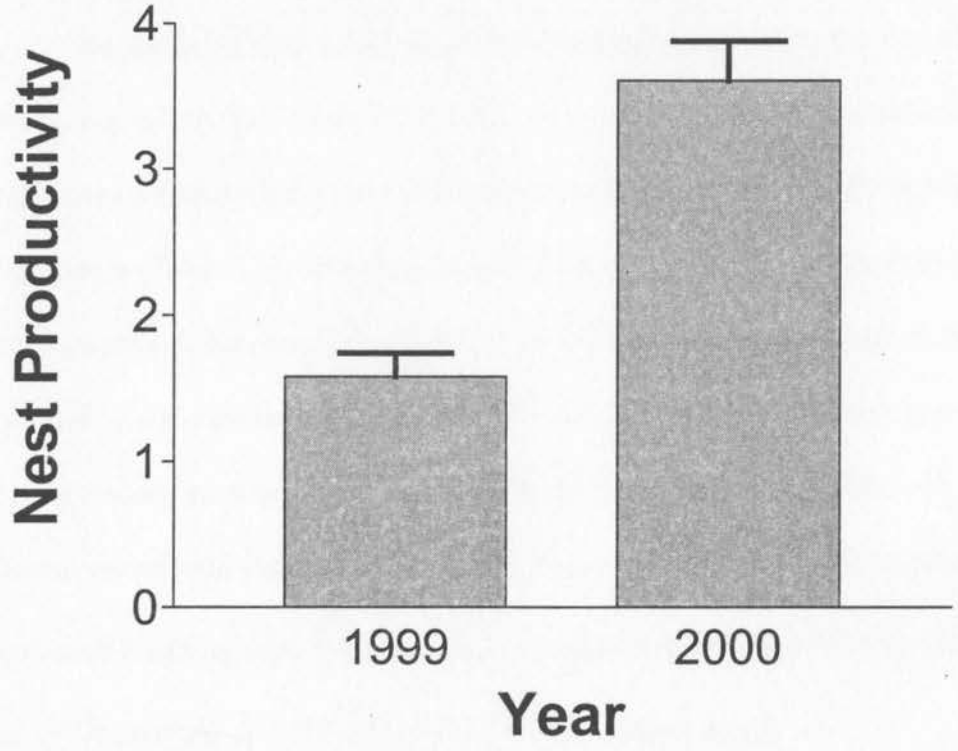

Figure 3.1. Burrowing owl productivity on the Pawnee National Grassland, 1999-2000. Productivity reflects number of young fledged per breeding attempt (1999: $n = 97$; 2000: $n = 100$). Bars on graph represent + 1 standard error.

Colony Scale

Burrowing owl breeding densities were best explained by the size of the occupied prairie dog colony (β = -0.48, CI = -0.68, -0.28; Table 3.4). All models within the 95% confidence set contained a colony size effect, and colony size had the highest relative importance (Table 3.5). Breeding density decreased with colony size despite an increase in the number of breeders ($\chi^2_1 = 3.89$, $P = 0.05$; Fig. 3.2). Active burrow density was included in a competing model (β = -0.00, CI = -0.01, -0.00); however, the addition of burrow density parameters explained little additional variation (Table 3.4). Breeding density varied with year (Wilk's Lambda: $F_{1,19} = 4.87$, $P = 0.04$). Colonies that supported breeding owls in both years had higher densities in 1999 than 2000 ($\bar{x}$ = 0.89, SE = 0.19, n = 20; $\bar{x}$ = 0.67, SE = 0.14, n = 21, respectively).

The best model for predicting colony success rates contained colony size (β = -1.32, CI = -2.19, -0.45) and the density of inactive burrows/ha (β = -0.02, CI = -0.05, -0.00; Table 3.4). R^2 values for the best model (0.24) and the global model (0.25) did not significantly differ. Colony size had a large importance value, suggesting it was a powerful predictor of nesting success (Table 3.5). Smaller colonies fared better, fledging more young per breeding attempt than larger sites (Fig. 3.2). Although habitat models performed poorly in reproductive analyses when colony size was ignored, relative importance measures suggest active and inactive burrow density effects may be of secondary importance in site selection.

The most parsimonious model for burrowing owl productivity included colony size (β = -0.92, CI = -1.63, -0.21) and inactive burrow density (β = -0.02, CI = -0.05, 0.00). Model likelihood did not significantly differ between the best model and the

Table 3.4. Habitat models (95% confidence sets) used to predict burrowing owl breeding densities and reproductive performance on occupied prairie dog colonies of the Pawnee National Grassland, 2000. Model subsets presented in order by relative strength of Akaike weights (w_i). R^2 values given for global models and best models as identified by AIC selection.

Demographic Parameter	Model	*n*	K	R^2	AIC_c	ΔAIC_c	w_i
Nesting Densities	size	23	3	53.4	-68.25	0.00	0.43
	size, aburrows	23	4		-67.83	0.42	0.35
	size, iburrows	23	4		-66.01	2.25	0.14
	size, iburrows, aburrows	23	5	58.9	-64.89	3.37	0.08
Nesting Success	size, iburrows	23	4	23.6	92.47	0.00	0.41
	size, aburrows	23	4		93.26	0.78	0.27
	size	23	3		94.34	1.87	0.16
	size, iburrows, aburrows	23	5	24.7	94.47	2.00	0.15
Productivity[a]	size, iburrows	23	4	45.0	55.59	0.00	0.40
	size	23	3		55.89	0.30	0.35
	size, aburrows	23	4		58.35	2.76	0.10
	size, iburrows, aburrows	23	5	45.0	58.88	3.29	0.08
	iburrows	23	3		59.80	4.21	0.05

[a] Data weighted by number of nesting pairs per colony.

Table 3.5. Relative importance of colony-level habitat variables to burrowing owl demography in northeastern Colorado, 2000. Importance values were calculated by summing Akaike weights (w_i) for all models containing the habitat parameter of interest.

Response Measure	Colony size (ha)	Inactive burrows/ha	Active burrows/ha
Nesting Densities	1.00	0.22	0.43
Nesting Success	0.99	0.56	0.43
Productivity	0.93	0.55	0.20

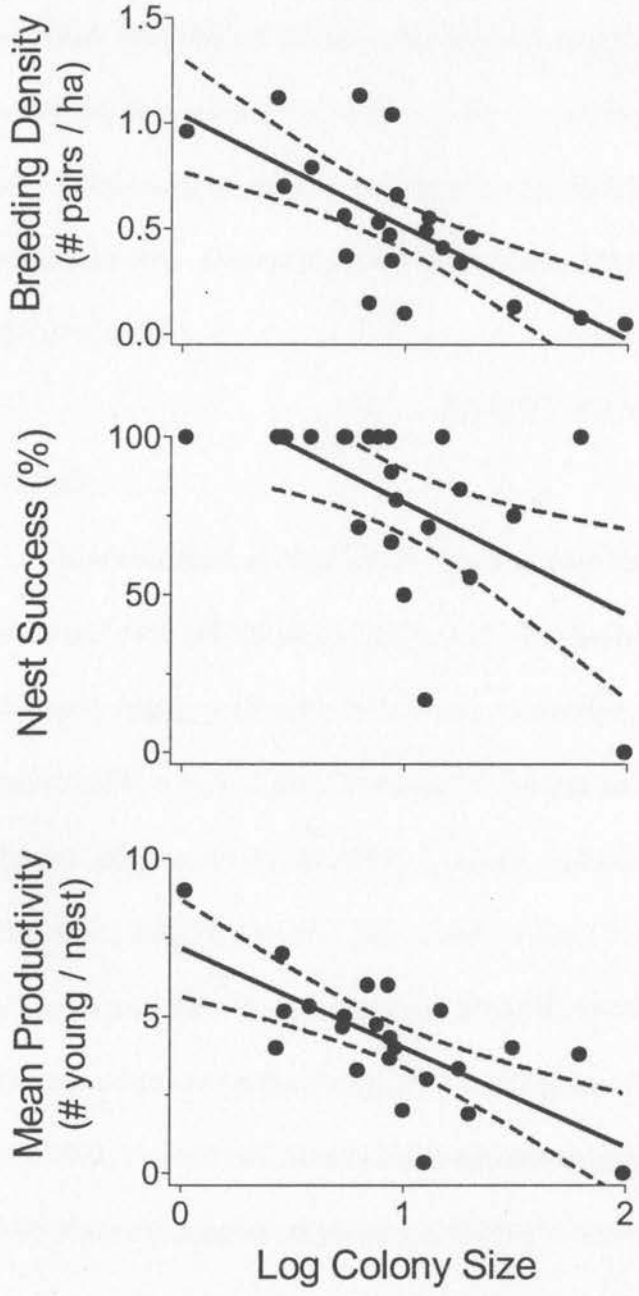

Figure 3.2. Burrowing owl breeding densities and reproductive performance in relation to the size of occupied prairie dog colonies, 2000. Points represent demographic data collected at individual colonies ($n = 23$). Solid lines indicate regression slopes and dashed lines the 95% confidence intervals.

model containing colony size only (Table 3.4). The relative importance of colony size was greater than that of either burrow density measure (Table 3.5). Like nesting success, productivity showed marked declines with increasing colony size (Fig. 3.2). R^2 values for the global and top models indicated better model fit than was present in nesting success analyses. Colony fledging rates differed between years (Wilk's Lambda: $F_{1,20} = 31.28$, $P < 0.001$).

DISCUSSION

Nest Scale

Habitat-based models had low w_i and explained little variation in observed success and productivity rates (Table 3.2). Predation and intraspecific competition can act independently or together in a density-dependent manner to regulate demography (Dewey and Kennedy 2001); however, reproduction remained unaffected by satellite burrow density or nearest-neighbor distance. Juveniles require multiple satellite mounds during post-fledging dispersal (King and Belthoff 2001); therefore, it is possible that satellite importance was not captured during the study period. Raptor studies found equivocal evidence for (Anthony 2001) and against (Rodriguez-Estrella and Ortega-Rubio 1993, Pedrini and Sergio 2001) nearest-neighbor effects. Green and Anthony (1989) observed nearest-neighbor effects for burrowing owls using badger burrows in Idaho; however, burrow density was low ($\bar{x}$ = 1.8 burrows /ha). Higher burrow availability on prairie dog colonies, coupled with opportunistic foraging (Chapter 2), likely precluded neighbor effects. Birds should select nest sites that reduce predation and competition in order to maximize fitness (Powell and Steidl 2000). Burrowing owls

arriving on the breeding grounds therefore may adjust nest placement in such a manner as to minimize the effects of competition and predation.

Annual fluctuations in reproductive performance are reported in the raptor literature (Steenhof et al. 1999, Desmond et al. 2000, McClaren et al. in review). Although year-based models performed poorly for nesting success analyses, productivity differed between years (Table 3.2, Fig. 3.1). Rainfall in 1999 (March-August = 35.7 cm) exceeded that of 2000 (March-August = 22.0 cm; NOAA 2001). Prolonged periods of inclement weather can lead to reduced nestling size and increased starvation in avian populations by limiting prey availability or reducing foraging efficiency (Murphy 1983, Dawson and Bortolotti 2000). Although the exposure risks differ for sheltered nesters (Kostrzewa and Kostrzewa 1990), flooding can be a significant source of mortality (Desmond 1991, Millsap and Bear 2000). Increased rates of starvation and flooding may have contributed to lower reproduction in 1999.

Colony Scale

Prairie dog colony size moderately influenced breeding densities and reproductive performance. Size was included in all models in 95% confidence sets (Table 3.4). Colony size also had consistently higher relative weights of evidence than those observed for either burrow density measure (Table 3.5). Decreases in breeding density with increasing colony size are reported (Hughes 1993, Desmond and Savidge 1996). Breeder scarcity may have played a role in observed trends. If owls arriving on the breeding grounds of the Pawnee are selecting for small sites, there simply may not be enough nesting pairs in the breeding population to fill in available habitat on the largest prairie dog colonies. Although the similarity in breeding numbers between years might suggest

habitat saturation, a lack of observed floater individuals and the presence of large expanses of unoccupied habitat do not support this position.

Reproductive performance showed similar declines with increasing colony size. My results differed from those observed by Ekstein (1999) and Desmond et al. (2000). Poor reproduction on large colonies does not appear to be a consequence of intraspecific interactions among nesting pairs or a lack of available burrows. Burrowing owl nests on small colonies had a higher likelihood of success and fledged more young on average (Fig. 3.2). Several factors may explain this trend. Small colonies may contain superior food resources; high breeding densities are indicative of high quality habitat. Higher rates of landscape fragmentation (cultivation) and human activity (recreational shooting, "off-road" use) may reduce reproductive performance on large, public prairie dog colonies (Chapter 4). It is also possible that unmeasured variables or those acting at spatial/temporal scales outside the scope of this study influenced breeding density and reproductive output.

Nest establishment has been linked to prairie dog activity levels (Desmond et al. 2000). Breeding pairs may nest in areas of high prairie dog activity because doing so reduces predation risk or because burrows in active regions are more likely to be well maintained. Although active burrow density was not in the top model for predicting nest densities, the addition of this parameter did not significantly reduce w_i. Contrary to expectations, and to what Desmond et al. (2000) reported for burrowing owls breeding in Nebraska, reproductive performance did not increase with prairie dog activity. The different responses to active burrow density measures may be attributed to regional variation in predation rates. High nesting success rates suggest predation was not a

significant source of owl mortality for burrowing owls breeding on the Pawnee in 2000. Few burrows exhibited evidence of predation, and only once did I observe a predator (badger) near the entrance of a burrowing owl nest.

Breeding densities of burrowing owls on the Pawnee were not associated with the density of inactive burrows on occupied colonies. All models containing inactive burrow density had low likelihood values. Burrow densities on prairie dog colonies can range from 50-300 burrows/ha (Archer et al. 1987), a far greater number than the 1.8 burrows/ha observed by Green and Anthony (1989) for owls using badger habitat in Oregon. Relative weights suggest a secondary role for inactive burrow availability in reproductive determination. The lack of overwhelmingly supportive w_i for the top reproductive models indicates other factors, such as perch availability, prey abundance, and vegetative cover may be more important.

MANAGEMENT IMPLICATIONS

Effective management of remaining burrowing owl populations requires a balance between maintaining a sizeable breeding population and maximizing reproductive performance of nesting pairs. Increasing the number of small, expanding prairie dog colonies will provide prospective breeders with a variety of potentially productive sites. As burrowing owls occupy the majority of active prairie dog colonies on the Pawnee, many of these emergent colonies would likely support nesting pairs, increasing the size of the breeding population. Maintaining a sizable pool of breeders will also help to minimize the effects of annual fluctuations in reproduction and episodic bouts of plague on population viability.

Although nests on large sites are more prone to failure and fledge fewer young on average, large colonies currently support the majority of nesting pairs. Minimizing the influence of habitat fragmentation and human disturbance on large colonies may help to enhance current population fitness while small colonies are being established. Regulating recreational shooting of black-tailed prairie dogs, a contributor to lower reproductive output in burrowing owls (Chapter 4), is a priority.

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CHAPTER 4

RESPONSE OF BREEDING BURROWING OWLS TO RECREATIONAL SHOOTING OF BLACK-TAILED PRAIRIE DOGS

The burrowing owl (*Athene cunicularia*) is a listed threatened and endangered species in Canada and is of regional concern in the United States (Haug et al. 1993, James and Espie 1997). Significant mortality and reduced reproductive output have been linked to human activity on the breeding grounds (Konrad and Gilmer 1984, Millsap and Bear 2000). Yet, despite extensive documentation, the magnitude and extent of disturbance effects and the mechanisms by which human activities contribute to population declines remain poorly understood (Haug et al. 1993, Holroyd et al. 2001).

The black-tailed prairie dog (*Cynomys ludovicianus*), a prominent nest-provider for burrowing owls (Desmond et al. 2000), is frequently targeted by recreational shooters. Prairie dog colonies in Wyoming, Colorado, and Nebraska are subjected to thousands of hunter use days (K. Gordon, Wyoming Cooperative Fish and Wildlife Research Unit, personal communication, J. Proctor, Predator Conservation Alliance, personal communication), and shooters killed more than 1 million prairie dogs in South Dakota in 2000 (L. Gigliotti, 2000. Prairie dog shooting in South Dakota (2000), South Dakota Game, Fish and Parks, Pierre, South Dakota, USA). Because shooting can affect avian

species directly through killing and indirectly through disturbance (Evans and Day 2001), burrowing owl populations occupying such sites may be susceptible to shooting effects. Traumatic injuries are a principle cause of raptor mortality (Keran 1981, Franson et al. 1995). Shooting fatalities may be significant, and are reported for numerous raptor species, including the New Guinea harpy eagle (*Harpyopsis novaeguineae*) (Watson and Asoyama 2001), ferruginous hawk (*Buteo regalis*) (Houston and Bechard 1984), and great horned owl (*Bubo virginianus*) (Franson and Little 1996). Although prairie dogs remain the primary target of recreational shooters using colony habitat, burrowing owl mortality is also reported (Butts 1973, Belthoff et al. 1995). Shooting mortality is sometimes compensatory (Burnham and Anderson 1984, Rexstad 1992) and sometimes additive (Smith and Willebrand 1999) to natural mortality in avian populations. If additive in raptor species, shooting mortality may exacerbate population declines.

The coincidence of peak shooting activity and the burrowing owl breeding season may leave nesting pairs prone to desertion, nest failure, and reduced productivity if shooting interferes with nesting and foraging activities. Human disturbances have been demonstrated to affect avian parental care (Fernandez and Azkona 1993), habitat use (Fletcher et al. 1999), and reproduction (White and Thurow 1985, Steenhof et al. 1999). Griebel (2000) noted increased clutch size for owls breeding on prairie dog colonies in the Buffalo Gap National Grassland where shooting is not permitted, as compared to owls nesting on adjacent lands subject to recreational shooting. If sufficient, the direct and indirect effects of recreational shooting on owl reproduction, survival, and recruitment may reduce the likelihood of population persistence. In the absence of immigration, sustainability of the resulting sink populations is unlikely (Koenen et al. 2000).

If species of concern are to be effectively conserved, mitigation of human disturbance is essential. Research will be of particular importance in helping to (1) identify the species affected by, and their response to, shooting and other human activities; and (2) understand how demography may be altered by such activities. For burrowing owls, few studies have directly compared demographic parameters under different disturbance regimes and intensities. A quantitative, comparative approach is needed to permit a more rigorous assessment of the effects of disturbances such as recreational shooting.

Here, I report on the relationship between recreational shooting and reproduction for burrowing owls breeding on prairie dog colonies in northeastern Colorado. Specific objectives were to (1) identify the prairie dog colony and landscape features influencing site selection by recreational shooters; (2) relate burrowing owl breeding numbers, success rates, and productivity data to the presence and intensity of recreational shooting activity; and (3) note instances of gunshot trauma to address shooting mortality.

STUDY AREA

Fieldwork was conducted on the Pawnee National Grassland, a 78,100-ha mosaic of public, private, state, and U.S. Department of Agriculture (USDA) research lands located in northeastern Colorado (Fig 4.1). Climate is typical of mid-continental semi-arid regions. Annual precipitation averages 321 mm, falling primarily as rain from April through June (Lauenroth and Sala 1992). Low humidity, high winds, and periodic severe drought characterize the summer breeding season. Perennial C_4 grasses dominate the moderately grazed landscape; blue grama (*Bouteloua gracilis*) and buffalo grass (*Buchlöe dactyloides*) are particularly abundant.

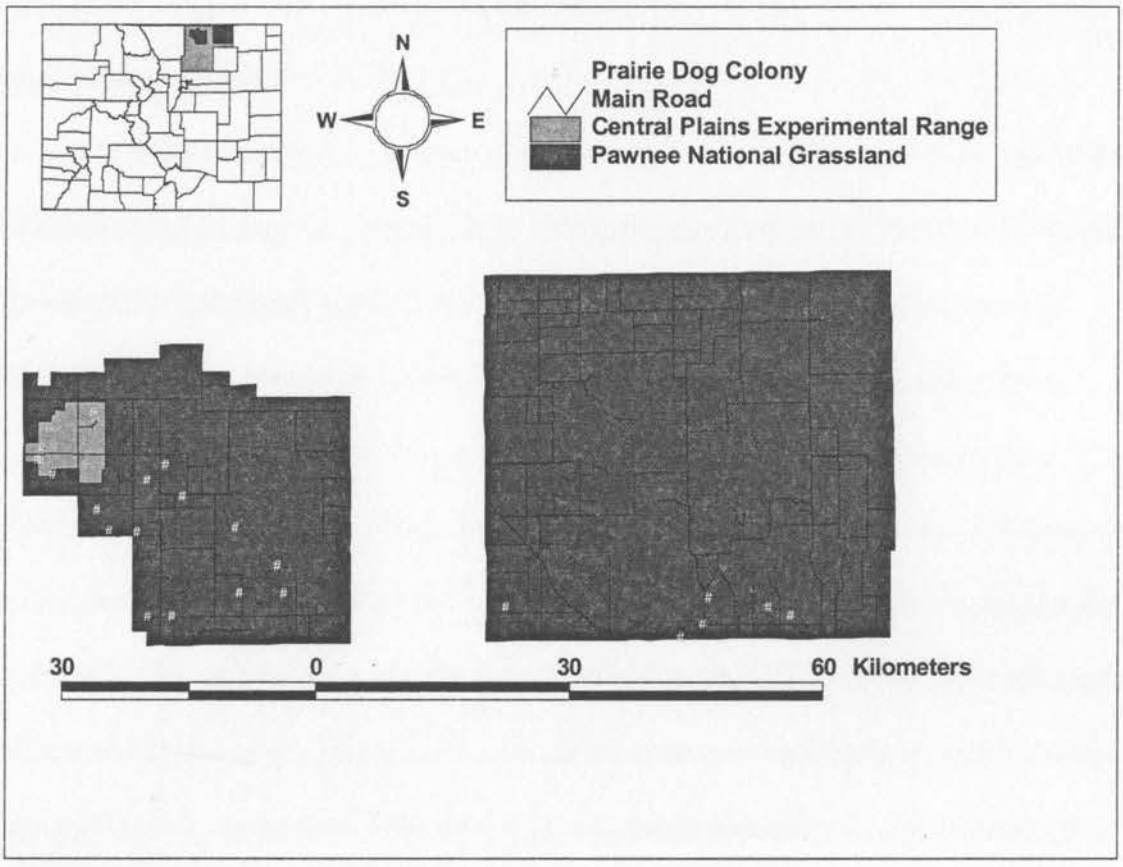

Figure 4.1. Black-tailed prairie dog colonies occupied by burrowing owls breeding on the Pawnee National Grassland, Weld County, Colorado (40°45'N, 104°30'W), 1999-2000.

METHODS

Monitoring Protocol

Breeding burrowing owls were monitored from 17 April through 3 August 1999 and from 9 May through 12 August 2000. The Colorado Division of Wildlife (J. Wagner, personal communication) and U.S. Forest Service (Ball 1998) provided locations of prairie dog colonies occupied by burrowing owls. I identified 207 nests using field observations and ground inspection of burrows; 10 nests located post-hatch were excluded from analyses to eliminate statistical bias associated with the inclusion of late-season successful pairs (Lehman et al. 1998). Occupied colonies were surveyed weekly and the breeding status of individual nests confirmed using: (1) repeated observation of a mated pair; (2) presence of eggshell fragments on or near the nest mound; and (3) visible nesting behaviors, such as marked decreases in aboveground female activity during the May-June incubation period, and feeding of female mates by adult males.

Demography

The number of nesting pairs per prairie dog colony was recorded, and reproductive output determined at each nest site. Nests were considered successful if one or more young reached a fledging age of 28 days (Zarn 1974). The maximum number of post-fledging young observed at the nest entrance provided minimum productivity estimates. A photographic key developed by Priest (1997) aided in age determination of young.

Burrowing owl mortality attributed to recreational shooting was noted during the 1999-2000 breeding season. When detected, the date, colony, and location of owl remains were recorded. External trauma indicative of gunshot wounds formed the basis

of diagnostic analyses (Franson and Little 1996). The presence of shot and/or prairie dog carcasses supported diagnostic conclusions. As some carcasses may have been scavenged between surveys and all intact carcasses not found, reported losses are likely a conservative estimate of true shooting mortality.

Shooting Classification

Prairie dog colony and habitat features were measured to establish shooter preferences (Appendix F). I determined land ownership for each prairie dog colony using existing land-use data. Surveyed colonies were classified as public, private, or USDA research land. State lands did not support prairie dog colonies occupied by burrowing owls and were ignored. I used a Global Positioning System (GPS) unit to map occupied colonies in May-June of 1999 and 2000; the outermost active prairie dog burrows delineated colony boundaries. GPS data were entered into PC Arc/Info 3.5 (ESRI 1997), a Geographic Information Systems (GIS). Colony size and nearest-colony distance measures were obtained directly from the GIS. Road maps and field observations were used to evaluate colony accessibility and designate colonies as: (0) inaccessible – reached by foot only; (1) moderately accessible – "off-road" or similar vehicle required on access road; or (2) highly accessible – main road present at colony perimeter.

In 1999, I classified colonies as "shooting" or "non-shooting" based on weekly field observations. Presence of (1) shooters at or within colony boundaries, (2) spent shell casings and shooting accessories, and (3) prairie dog carcasses with identifiable gunshot trauma served as the criteria used in establishing colony shooting status. As presence or absence of recreational shooting was simply noted and no attempt made to estimate relative amounts of shooting activity, I did not distinguish among shooting sites.

In addition to noting shooting presence or absence on occupied colonies in 2000, shooting activity was further quantified to rank colonies based on shooting intensity. I walked random transects and access roads during weekly surveys and recorded all shooting-evidence materials (Appendix G). Evidence used in assigning colony ranks followed that used in establishing shooter presence/absence. Visual inspection determined shell condition. Rusted, tarnished, or otherwise visibly old shells were excluded from counts. Presence of dirt within a shell casing did not preclude its use, as shells frequently were found on well-traveled 2-track roads. I assumed recreational shooters on the Pawnee National Grassland had firing (110 rounds/day) and prairie dog kill rates (40-50%) similar to that reported for the Buffalo Gap National Grassland (G. Schenbeck, Wildlife Coordinator, Northern Great Plains Planning Team, unpublished data). For each survey, the minimum number of shooters necessary to generate observed evidence was calculated. Based on this methodology, a value of one would be assigned to a survey in which one recreational shooter, five shell casings, and two prairie dog carcasses were observed. Survey values were totaled by colony and divided by three, the number of shooting evidence categories. Shooting ranks included: 0 = no shooting; 0-1 = low intensity shooting; >1 = high intensity shooting.

Statistical Analyses

Frequency analyses tested for an association between recreational shooting and land ownership. I noted shooting activity (present/absent) and land ownership (public/private), and recorded the number of prairie dog colonies in each of the four possible category combinations. Private and USDA research lands required permission prior to site access and use by recreational shooters. For this reason, both ownership

categories were considered representative of private lands. Fisher's exact test (2-tailed) was used to analyze these frequencies. The Fisher statistic was preferred to the Chi-square statistic due to low overall sample size ($n = 25$ colonies).

Logistic regression identified predictors of recreational shooting activity. Shooting presence/absence served as the response variable. Prairie dog colony size, distance to the nearest neighboring colony, and colony accessibility were the independent variables. Predictors were tested for collinearity. If two variables were significantly correlated ($P < 0.05$), I retained the variable that had a smaller Pearson coefficient (r) with respect to remaining model predictors.

A repeated-measures analysis of variance (ANOVA) tested for year and shooting effects on the number of nesting pairs per occupied colony. I considered nest numbers a repeated measure as counts occurred on the same experimental units (i.e. colonies) in both years. Colonies with <2 years of data ($n = 4$) were excluded. The number of breeding pairs was the response variable and shooting presence/absence the primary model predictor. Year served as the repeated measure. A colony size effect on nesting numbers was detected (Chapter 3); therefore, size was included as a model covariate.

The relationship between recreational shooting and nesting success was examined using a nonlinear mixed ANOVA. Nonlinear analysis permitted the inclusion of a random colony effect into the binomial-based model and was necessary to correct for model overdispersion. I included the colony variable for two reasons: (1) surveyed colonies represented a random subsample of the total breeding population; and (2) inclusion of the colony effect adjusted sample size to reflect the number of colonies, and not nests, sampled. Nesting success was the response variable. Shooting

presence/absence was the primary predictor. A year effect incorporated into the initial model assessed temporal variation in success rates. Colonies with few breeding pairs unduly influenced results; therefore, I omitted single-nest colonies from analyses ($n = 6$).

Productivity in relation to shooting activity was assessed by mixed model ANOVA. Colony productivity (mean young fledged/breeding attempt) served as the response variable. Weighting of reproductive estimates by the number of nesting pairs avoided bias in results. A year term was included in the model to assess temporal effects on productivity analyses. Significance of the year effect was determined by the *F*-statistic of the model.

The relationship between shooting intensity and nesting success and productivity was analyzed during 2000. Colony success rates were examined using a logistic analysis. The number of successful nests/total colony nests served as the response variable and shooting intensity was the model predictor. The Hosmer and Lemeshow statistic measured model lack-of-fit. The productivity-shooting intensity relationship was assessed using the same methodology employed in productivity by shooting presence/absence analyses with two notable exceptions: (1) the year effect was dropped from the intensity-based analysis; and (2) shooting intensity replaced shooting presence/absence as the primary model predictor.

Statistical analyses were conducted using SAS v. 8.1 (SAS Institute 2000). The Shapiro-Wilk statistic (PROC UNIVARIATE) tested normality assumptions for response and predictor variables. Appropriate transformations were applied when necessary to correct for data non-normality. I considered results significant at $P < 0.05$. Reported values are presented as means $\pm$ SE unless otherwise noted.

RESULTS

Site Selection

Recreational shooting varied with land ownership (Fisher's exact test: df = 1, $P <$ 0.01). Shooters exclusively used public lands, with two-thirds of public prairie dog colonies experiencing recreational shooting activity. Because no shooting occurred on private lands, I regressed shooting data on predictor variables for public sites only ($n = 15$ colonies). The distance to the nearest neighboring colony decreased with increasing colony size ($r = -0.54$, $P = 0.05$); therefore, I excluded nearest-neighbor measures from preference analysis. Shooting activity was not associated with prairie dog colony size ($\chi^2_1 = 0.3$, $P = 0.57$) or accessibility ($\chi^2_1 = 1.2$, $P = 0.28$).

Shooting Effects

Prairie dog colonies subject to recreational shooting activity tended to support more nesting pairs of burrowing owls; however, differences were not significant (Table 4.1). Colony size did not influence breeding numbers when all colonies were considered ($F_{1,18} = 0.25$, $P = 0.62$). The number of nesting pairs on colonies smaller than 30 ha ($n =$ 17) was positively correlated with colony size ($F_{1,15} = 4.47$, $P = 0.05$). The average number of nesting pairs/colony varied with time (Wilk's lambda: $F_{1,18} = 6.78$, $P = 0.02$); however, I believe this observed decline in breeding numbers was likely an artifact of statistical analysis. When single-nest colonies were included in mean calculations, nesting numbers in 1999 and 2000 remained identical ($\bar{x} = 4.52$, SE = 0.61, $n = 23$; $\bar{x} =$ 4.52, SE = 0.48, $n = 23$, respectively).

Reproductive performance varied with recreational shooting activity. Nests on non-shooting sites had a higher, albeit marginal, rate of success (Table 4.1). Year weakly

Table 4.1. Burrowing owl breeding numbers and reproductive output on prairie dog colonies ($n = 25$) with and without recreational shooting activity, 1999-2000.

	Shooting present			Shooting prohibited					
Response variable	$\bar{x}$	SE	n	$\bar{x}$	SE	n	F	df[a]	P
Nesting pairs	5.65	0.83	10	3.91	0.55	11	2.47	18	0.13
Nesting success (%)	65.91	0.05	88[b]	75.73	0.04	103[b]	-1.62[c]	39	0.11
Productivity (1999)[d]	1.10	0.26	39[b]	1.79	0.20	58[b]	4.36	21	0.05
Productivity (2000)[d]	3.16	0.51	50[b]	4.06	0.51	50[b]	1.57	21	0.22

[a] Denominator degrees of freedom.

[b] Sample size reflects breeding pair data nested within colonies.

[c] Result based on t-statistic.

[d] Number of young fledged/nest attempt.

influenced nesting success ($t_{39} = 1.83$, $P = 0.07$). Breeding pairs in 1999 had a lower rate of success than did pairs nesting in 2000 ($\bar{x} = 65.95\%$, SE = 0.05, $n = 94$; $\bar{x} = 76.29\%$, SE = 0.04, $n = 97$, respectively). Nests in 2000 fledged >2 more young per breeding attempt than did their 1999 counterparts ($F_{1,43} = 20.69$, $P < 0.001$). Due to this strong annual effect on productivity, data were analyzed separately for 1999 and 2000. Shooting activity negatively influenced productivity in 1999 (Table 4.1); 2000 analyses showed a similar but non-significant trend (Table 4.1). The number of colonies supporting recreational shooting activity did not differ between years ($P = 0.19$).

Nesting success did not significantly differ with the intensity of recreational shooting ($\chi^2_2 = 2.71$, $P = 0.26$; Fig. 4.2). Success rates for nests on colonies of low to moderate shooting activity ($\bar{x} = 70.83$, SE = 0.09, $n = 24$) were similar to those for nests on colonies frequented by recreational shooters ($\bar{x} = 69.23$, SE = 0.09, $n = 26$). Productivity showed a similar response. Although nests on non-shooting colonies fledged nearly one more young per breeding attempt than did nests on shooting sites, productivity was unaffected by shooting intensity ($F_{2,20} = 0.75$, $P = 0.49$; Fig. 4.2).

Three adult owls (1% of the 1999-2000 breeding population) died from gunshot trauma. Fatalities occurred on separate prairie dog colonies and always within 1-2 m of a satellite mound in the nest vicinity. At least one fatality was associated with a period of intense shooting activity. A 19 June 2000 survey of an eastern colony yielded a dead burrowing owl among 1 13-lined ground squirrel (*Spermophilus tridecemlineatus*), 1 desert cottontail (*Sylvilagus audubonii*), and 34 prairie dog carcasses.

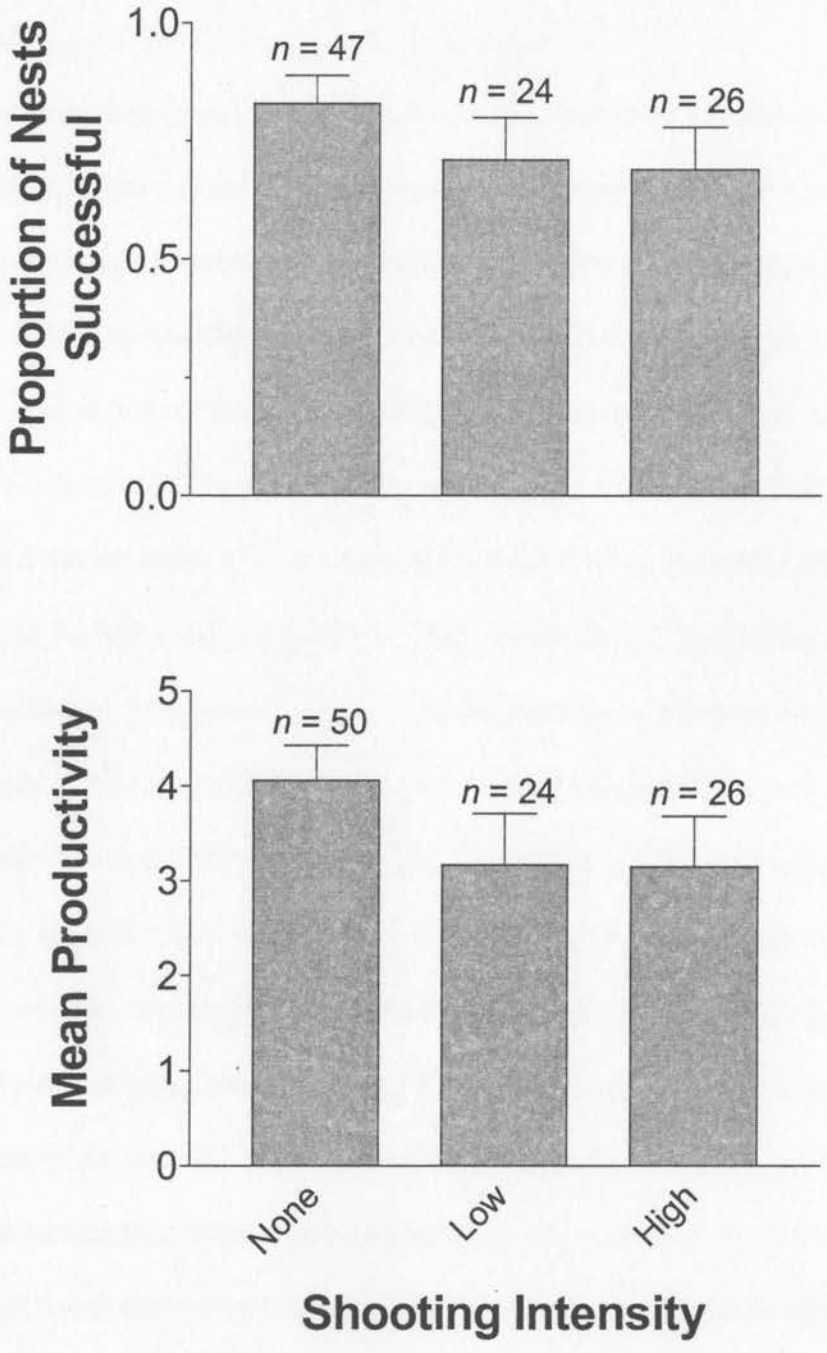

Figure 4.2. Nesting success and productivity of burrowing owls breeding in northeastern Colorado as a function of recreational shooting intensity, 2000. Vertical bars represent +1 SE. Numbers above bars indicate number of nests sampled.

DISCUSSION

Site Selection

Land ownership primarily governs recreational shooting patterns. Shooting is common where prairie dog colonies are abundant. Both public and private lands offer recreational shooting opportunities. On the Pawnee National Grassland, public lands provide a supply of accessible colonies. Private and USDA research lands support numerous colonies, but restricted public access precludes their use by recreational shooters. G. Schenbeck (Wildlife Coordinator, Northern Great Plains Planning Team, unpublished data) reported extensive recreational shooting on the public prairie dog colonies of the Buffalo Gap National Grassland. Private lands can support substantial shooter populations, as is evident in South Dakota where use of private lands exceeds that of public lands (L. Gigliotti. 2000. Prairie dog shooting in South Dakota (2000), South Dakota Game, Fish, and Parks, Pierre, South Dakota, USA). The abundance of prairie dog habitat in South Dakota and the potential for revenue generation may explain this trend. Recreational shooting activity on the Pawnee National Grassland was not influenced by measured habitat parameters; shooters used the majority of available public sites. Patterns of site use may therefore be more a response to recreational limitations than active selection for preferred colony habitat.

Recreational shooters exhibited strong site fidelity; most colonies experiencing shooting activity in 2000 were also shot in 1999. Annual prairie dog colony surveys documented shooting at several colonies for more than a decade (M. Ball, U.S. Forest Service, personal communication). Although observations such as shooter avoidance of a colony extending onto private land suggest shooting decisions involve some measure of

site attractiveness, shooters ultimately may base decisions on previous success rates (i.e. prairie-dog kill rates) and observed hunter-use patterns.

Shooting Effects

It is unlikely that shooting activity promoted colony use by nesting burrowing owls. If shooting enhances site use, owl breeding numbers should fluctuate with changes in shooting presence and intensity. No such pattern was observed. Nest numbers remained consistent within colonies, including two colonies where shooting status differed between years. While colony reuse is high, banding data suggest that many owls are new individuals; therefore, site fidelity cannot sufficiently explain the tendency for shooting sites to support more nesting pairs. Larger breeding populations may reflect the influence of some unmeasured burrow, colony, or landscape feature.

Recreational shooter presence on occupied prairie dog colonies was associated with declines in nesting success and productivity. Shooting mortality may have been a factor, for it invariably determined nest fate. All nests losing a breeding adult to shooting failed to fledge young. Although the number of owls lost to recreational shooting on the Pawnee National Grassland represented a fraction of the total breeding population, given the low probability of detection of dead raptors (Koenen et al. 2000), it is likely that these results provide a conservative estimate of shooting-related mortality. Recreational shooting may also have indirectly contributed to reductions in reproductive performance and available nesting habitat. Pedrini and Sergio (2001) noted diminished reproductive success at golden eagle (*Aquila chrysaetos*) nests lacking both adults. Lower burrowing owl productivity on shooting sites may have resulted from changes in foraging patterns, nest attendance, or other behaviors critical to reproductive performance.

The lack of a linear response to shooting intensity suggests that other factors contributed to reproductive determinations. Although reproduction was higher on prairie dog colonies with no recreational shooting activity relative to colonies subject to frequent shooter visits, shooting alone cannot explain the observed patters. Precipitation resulted in differential rates of nest failure and desertion among colonies (Woodard, unpublished data). Spatial variation in weather, prey availability, or predator populations may have contributed to reduced nesting success and productivity on colonies of low to moderate shooting activity.

MANAGEMENT IMPLICATIONS

Despite an ability to occupy and successfully breed in moderately fragmented and disturbed landscapes (Millsap and Bear 2000, Orth and Kennedy 2001), burrowing owls remain susceptible to human activity. Although habitat loss is a primary concern, harassment, motor vehicles, pesticides, and recreational shooting contribute to local mortality and remain continued threats to breeding populations (Haug et al. 1993). Quantifying the effects of human activities on raptor demography can provide information necessary for effective management. For example, recovery of the southeastern Alaska bald eagle (*Haliaeetus leucocephalus*) breeding population is attributed to a halt in the bald eagle bounty (1917-1953) that killed an estimated 150,000 individuals (Jacobson and Hodges 1999). Results suggest that recreational shooting may exacerbate the continued decline of burrowing owls and therefore its management should be incorporated into conservation plans.

Maintaining an abundance of active prairie dog colonies will provide recreational shooters with alternative sites. Although occupation rates are quite high, all colonies are

not likely to be occupied by breeding owls (Plumpton and Lutz 1993, personal observation). Reducing shooting activity on colonies historically productive or preferred by burrowing owls will minimize unnecessary direct mortality and indirect reproductive losses, and may help to stabilize breeding populations. Restrictions during nest placement in March-April and during the July nestling period when owl activity and energetic demands are greatest may be effective in reducing shooting effects on burrowing owls.

As the loss, degradation, and fragmentation of habitat continue to reduce nest-site availability and habitat quality, identifying and mitigating additional sources of conflict will be critical to sustaining burrowing owl populations. Educating the public on the merits of raptor management has shown promise, and may be an effective tool in reducing conflict. Burrowing owl harassment, a significant source of nest failure in Florida breeding populations, decreased dramatically following the incorporation of raptor education programs into the Cape Coral school system (Millsap and Bear 2000). Minimizing owl-shooter conflicts should benefit breeding owls because continued losses will inevitably lead to reductions in suitable breeding sites.

The Colorado Division of Wildlife imposed a recreational shooting ban on prairie dog colonies of the Pawnee National Grassland in September 2001 (J. Dennis, Colorado Division of Wildlife, personal communication). Monitoring programs should be initiated to compare population and reproductive estimates prior to and following shooting restrictions.

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APPENDIX A

Invertebrate prey identified in burrowing owl castings collected on the Pawnee National Grassland, Colorado, 2000.

Family	Species
ARACHNIDA	
Eremobatidae	Unidentified "A"
Salticidae	Unidentified "A"
INSECTA	
Acrididae	*Arphia conspersa* *Melanoplus bivitattus* *Melanoplus differentialis* *Trachyrhachus kiowa* *Xanthippes corallipes* Unidentified "A"
Carabidae	*Amara sp.* *Chlaenius sp. A* *Chlaenius sp. B* *Euryderus sp.* *Geopinus incrassatus* *Harpalus calignosis* *Helluomorphoides sp.* *Loxandrus sp.* *Pasimachus elongatus* *Peairs alfalfa* *Piosoma sp.* Unidentified "A" Unidentified "B" Unidentified "C" Unidentified "D" Unidentified "E" Unidentified "F" Unidentified "G"
Cerambycidae	*Monolema annulata* *Prionus integer* Unidentified "A"
Chrysomelidae	*Crptocephalus confluentus* Unidentified "A"
Cicindelidae	Unidentified "A" Unidentified "B"

Curculionidae	*Sphenophorus cicatristiatus*
	Thecesternus sp.
	Unidentified "A"
Formicidae	*Camponotus noveboracensis*
	Formica neogagates
	Myrmica emeryana
Gryllacrididae	Unidentified "A"
	Unidentified "B"
Gryllidae	*Gryllus sp.*
Halictidae	*Agapostemon sp.*
	Unidentified "A"
Histeridae	*Spilodiscus sp.*
Hydrophilidae	*Hydrophilus triangularis*
Ichneumonidae	Unidentified "A"
	Unidentified "B"
Scarabaeidae	*Aphodius sp.*
	Canthon pilularius
	Canthon praticola
	Geotrupes sp.
	Ligyrus gibbosus
	Phaneus vindex
	Phyllophaga sp.
	Polyphylla sp.
Silphidae	*Heterosilpha ramosa*
	Nicrophorus sayi
Tenebrionidae	*Eleodes extricata*
	Eleodes fusiformes
	Eleodes hispilabris
	Eleodes obscura
	Eleodes obsoleta
	Eleodes opaca
	Eleodes tricostata
	Embaphion planum
	Stenosides anastomosis
	Trimytis pruinosis
	Unidentified "A"

Unidentified	Unidentified "A" Unidentified "B" Unidentified "C" Unidentified "D"
MALACOSTRACA	
Cambaridae	*Orconectes immunis*

APPENDIX B

Vertebrate species identified in burrowing owl castings collected on the Pawnee National Grassland, Colorado, 2000.

Scientific Name	Common Name
AVES	
Calamospiza melanocorys	Lark Bunting
Eremophila alpestris	Horned Lark
MAMMALIA	
Geomys bursarius	Plains Pocket Gopher
Microtus ochrogaster	Prairie Vole
Microtus pennsylvanicus	Meadow Vole
Onychomys leucogaster	Northern Grasshopper Mouse
Perognathus flavescens	Plains Pocket Mouse
Peromyscus maniculatus	Deer Mouse
Spermophilus tridecemlineatus	Thirteen-lined Ground Squirrel
Thomomys talpoides	Northern Pocket Gopher
REPTILIA	
Phrynosoma douglasii	Northern Short-horned Lizard

APPENDIX C

Reproduction and nest-level attributes at burrowing owl breeding sites, 1999.

Colony	Nest #	Nest-level Parameters		Reproductive Output	
		Satellite burrow density (30-m radius)	Nearest-nesting neighbor (m)	Nest successful?[a]	# Young fledged
5	44	29	202.89	0	0
	98	44	202.89	1	3
8	45	36	68.04	0	0
	46	38	46.60	1	2
	47	34	64.08	1	1
	48	38	75.86	1	3
	49	32	75.86	1	2
	50	30	93.25	1	2
	51	26	137.87	0	0
	52	46	29.76	1	1
	85	19	139.76	1	1
	97	28	91.99	1	3
	101	38	29.76	1	1
	102	42	46.60	1	1
13	68	39	141.56	1	1
	76	35	48.63	1	4
	77	34	63.02	1	2
	78	37	61.86	0	0
	80	35	48.63	1	3
	81	33	77.79	0	0
	82	36	111.30	0	0
	94	38	78.29	1	4
	95	37	78.29	1	2
17	56	20	65.92	1	5
	57	28	26.60	1	1
	58[b]	18	48.87	1	2
	59	19	278.01	1	5
	83	22	42.50	1	2
	84[b]	26	26.60	ND[c]	ND[c]
22	8	9	284.75	1	2
	9	19	145.88	1	4
	10	20	145.88	0	0
30	53	34	86.36	1	4
	54	35	86.36	0	0
35	55	80	220.20	0	0
	96	24	220.20	1	4
	107	35	428.18	1	1
51	19	10	40.93	0	0
	20	14	40.93	0	0
	21	19	114.71	0	0
	22	24	91.85	1	2
	23	20	95.65	1	1
	24	22	104.05	1	1
	86[b]	21	91.85	0	0
	106	23	114.71	1	2
62	66	30	223.32	0	0
	92[b]	17	223.32	1	4
72	43	15	5226.49	0	0

74	60	18	82.93	0	0
	61	19	75.27	1	2
	62	12	157.17	0	0
	63	17	75.43	0	0
	64	24	69.83	0	0
	65	29	69.83	1	1
	93	18	75.43	1	3
	105[b]	15	246.44	1	3
76	25	27	72.21	1	4
	26	16	72.21	0	0
	27	23	100.98	1	1
	28	17	23.39	0	0
	29	16	23.39	0	0
	75	18	110.93	1	3
	87	15	124.47	1	1
78	34	24	83.77	1	2
	35	26	80.67	0	0
	36	32	150.64	0	0
	89	41	80.67	1	3
	90	31	83.77	1	4
79	40	25	152.41	0	0
	41	28	152.41	1	2
81	37	16	51.61	1	4
	38	21	37.33	0	0
	39	14	37.33	1	3
	99	19	51.61	1	2
	100	8	67.10	1	1
82	32	15	59.99	0	0
	33	7	59.99	0	0
	108	7	102.20	0	0
83	11	28	163.19	0	0
	12	18	163.19	1	3
100	42	39	ND[c]	1	1
131	3	10	27.76	1	7
	4	16	24.60	1	3
	5	14	25.20	1	1
	6	16	47.86	1	1
	18[b]	9	111.93	ND[c]	ND[c]
	103	16	25.20	1	1
	104	18	24.60	1	2
132	1	24	71.94	0	0
	2	37	46.40	0	0
	91[b]	26	46.40	1	2
271	7	29	52.04	1	5
	30	39	52.04	0	0
272	13	22	67.68	1	1
	14	22	78.19	1	3
	15	23	50.13	1	5
	16	14	38.91	1	4
	17	18	38.91	1	1
	31	22	66.11	1	1
501	69	23	71.31	1	4

	70	36	59.22	1	2
	71	18	59.22	0	0
	72	27	79.74	0	0
	73	26	183.05	1	2

[a] 0 = failed nest; 1 = successful nest.

[b] Nest excluded from reproductive estimates and analyses as it was located post-hatch.

[c] Nest variable could not be determined.

APPENDIX D

Reproduction and nest-level attributes at burrowing owl breeding sites, 2000.

Colony	Nest #	Nest-level Parameters		Reproductive Output	
		Satellite burrow density (30-m radius)	Nearest nesting neighbor (m)	Nest successful?[a]	# Young fledged
5	24	30	194.22	0	0
	42	27	148.85	0	0
	43	26	795.33	0	0
	83	39	148.85	0	0
	84	45	195.80	0	0
8	34	35	127.95	0	0
	35	35	72.71	1	2
	36	18	72.71	1	6
	38	33	105.54	1	2
	39	37	95.34	1	3
	40	24	95.34	0	0
	41	30	76.27	1	4
	85	26	127.95	0	0
	86	27	76.27	0	0
13	10	35	52.25	0	0
	29	35	52.25	1	2
	30	37	199.72	0	0
	31	26	110.97	0	0
	88	31	142.87	0	0
	111	32	110.97	0	0
17	62	21	123.49	1	3
	63	24	123.49	1	2
	64	20	72.22	0	0
	65	19	134.65	0	0
	66	29	72.22	1	4
	104	24	161.37	1	7
	112	21	161.37	1	5
22	6	11	185.07	1	4
	7	22	140.08	1	5
	8	26	140.08	1	5
	9	11	201.56	1	5
30	87	35	2859.57	1	6
35	33	42	380.60	1	1
	105	35	268.03	1	4
	106	29	268.03	1	3
	107	25	197.52	1	3
	108	25	197.52	1	8
51	47	15	190.60	1	5
	48	20	112.86	1	4
	49	22	112.86	1	2
	50	18	108.44	1	4
	51	24	71.09	0	0

	54	25	79.72	1	5
	55	15	79.72	1	2
	101	29	71.09	1	4
	103	18	87.26	1	7
62	52	33	60.90	1	8
	56	18	236.56	1	6
	57	13	312.24	1	4
	58	18	113.71	1	6
	82	21	60.90	1	2
	110[b]	20	113.71	ND[c]	ND[c]
74	59	24	62.47	1	9
	60	13	62.47	1	3
	61	25	110.91	1	6
	109[b]	18	83.56	0	0
76	19	19	98.55	0	0
	20	20	72.93	1	5
	23	14	98.55	1	2
	25	18	50.88	0	0
	90	22	67.23	1	8
	95	17	67.23	1	3
	96	26	50.88	1	5
78	16	22	109.59	1	6
	17	29	62.60	0	0
	18	21	131.92	1	5
	92	30	34.61	1	4
	93	31	34.61	1	5
	94[b]	30	138.41	1	6
79	74	27	85.09	1	5
	75	22	85.09	1	5
81	26	26	67.72	1	8
	27	19	67.72	1	6
82	44	18	75.86	1	5
	45	24	66.31	1	2
	46	19	66.31	1	5
83	11	28	1928.12	1	2
	12	20	1841.58	0	0
103	67	8	151.67	0	0
	68	18	72.15	1	5
	69	15	126.87	1	1
	70	20	72.15	1	5
	71	20	221.54	1	4
	72	24	227.75	1	5
131	76	18	71.16	1	5
	77	17	70.58	1	8

	78	16	68.84	1	8
	97	18	71.93	1	1
	98	11	104.78	1	5
	102	15	68.84	1	4
132	79	29	40.30	1	3
	80	33	103.84	1	4
	81	22	40.30	1	7
271	3	26	212.62	1	6
	4	37	109.80	1	7
	5	17	109.80	0	0
272	1	21	82.18	1	7
	2	27	96.02	1	5
	99	25	82.18	1	4
301	28	19	1595.38	1	9
501	13	27	96.49	1	5
	14	24	96.49	1	9
	15	16	191.08	1	2
	113	25	236.73	0	0

[a] 0 = failed nest; 1 = successful nest.

[b] Nest located post-incubation (excluded from analyses to eliminate reproductive bias).

[c] Nest fate could not be determined.

APPENDIX E

Burrowing owl breeding densities and habitat characteristics of occupied prairie dog colonies, 1999-2000.

Colony	Area (ha)		Total burrows/ha	% Active burrows/ha	# Nests		Breeding density (nests/ha)	
	1999	2000	2000	2000	1999	2000	1999	2000
5	81.60	97.40	135.18	30.61	2	5	0.02	0.05
8	13.78	19.67	146.77	27.11	12	9	0.87	0.46
13	5.51	12.37	127.33	32.41	9	6	1.63	0.49
17	14.30	12.74	70.73	31.25	6	7	0.42	0.55
22	5.58	7.57	70.74	23.33	3	4	0.54	0.53
30	3.26	6.89	137.93	38.46	2	1	0.61	0.15
35	40.49	61.75			3	5	0.07	0.08
51	8.66	8.67	55.41	29.79	8	9	0.92	1.04
62	30.34	14.72	79.93	26.55	2	6	0.07	0.41
72	12.07				1		0.08	
74	9.27	8.50	69.56	44.07	8	4	0.86	0.47
76	6.34	6.21	78.99	16.42	7	7	1.10	1.13
78	7.99	9.13	112.00	30.53	5	6	0.63	0.66
79[a]	5.42	5.42	91.95	0.00	2	2	0.37	0.37
81	0.22	2.85	71.63	27.78	5	2	22.49	0.70
82	1.79	2.68	79.59	40.00	3	3	1.67	1.12
83	3.77	9.93	79.58	40.00	2	1	0.53	0.10
100	14.01				1		0.07	
103		17.70	47.75	44.44		6		0.34
131	1.86	2.91	59.69	33.33	7	6	3.77	2.06
132	3.25	5.32	102.56	31.03	3	3	0.92	0.56
271	5.22	8.69	119.08	58.42	2	3	0.38	0.35
272	2.95	3.79	79.59	45.00	6	3	2.03	0.79
301		1.04	99.48	36.00		1		0.96
501	17.29	30.90	63.66	40.00	5	4	0.29	0.13
Total	294.98	356.84			104	103		
$\bar{x}$	12.83	15.51	89.96	33.02	4.52	4.48	1.76	0.59
SD	17.72	21.95	28.60	11.59	2.94	2.37	4.60	0.46

[a] Colony lost to sylvatic plague during 2000 breeding season. 2000 measurements based on 1999 colony size estimate.

APPENDIX F

Land status, colony attributes, and recreational shooter use of prairie dog colonies occupied by breeding burrowing owls.

Colony	Colony Characteristics				Shooting Activity		
	Land Ownership	Mean Size (ha)	Accessibility[a]	Nearest Colony (km)	Presence/Absence		Intensity
					1999	2000	2000
5	Public	89.50	1	1.61	Yes	Yes	High
8	Public	16.73	1	1.61	Yes	Yes	Low
13	Public	8.94	2	2.50	No	No	None
17	Public	13.52	1	20.35	No	Yes	Low
22	CPER	6.58	1	1.04	No	No	None
30	Public	5.07	2	2.50	No	No	None
35	Public/Private	51.12	0	2.71	No	No	None
51	Public	8.67	2	4.95	Yes	Yes	High
62	Public	22.53	1	2.54	Yes	Yes	High
72	Public	12.07	0	2.91	No		Low
74	Public	8.88	1	2.54	No	Yes	Low
76	Public	6.27	2	3.80	Yes	Yes	Low
78	Public	8.56	1	2.51	Yes	Yes	None
79	Public	5.42	1	3.16	Yes	No	None
81	Public	1.54	0	2.51	No	No	None
82	Public	2.24	1	6.14	Yes	No	None
83	CPER	6.85	1	1.45	No	No	None
100	Private	14.01	2	ND[b]	No		None
103	CPER	17.70	1	1.49		No	None
131	Private	2.38	2	2.61	No	No	None
132	Private	4.29	2	2.61	No	No	None
271	CPER	6.96	1	0.13	No	No	None
272	CPER	3.37	1	0.13	No	No	None
301	CPER	1.04	1	1.49		No	None
501	CPER	24.10	1	4.81	No	No	None

[a] (0) inaccessible – reached by foot only; (1) moderately accessible – "off-road" vehicle required; or (2) highly accessible – main road present at colony perimeter.

[b] Distance to nearest-neighboring colony could not be determined.

APPENDIX G

Recreational shooting evidence observed during weekly owl surveys on occupied prairie dog colonies.

Colony	Date	Shooting Evidence	Location
5	06/10/00	Shells (50)	2-track road along southern boundary
	06/19/00	Shells (5), Recreational Shooter	2-track road along southern boundary
	07/23/00	Shells (3), Recreational Shooter	2-track road (10-20m from nest 84)
8	06/19/00	Dead Prairie Dog (34), Burrowing Owl (1), Cottontail (1), and 13-lined Ground Squirrel (1)	Base of hill in western portion of colony
17	06/02/00	Shells (3), Shell Rack (1), Shell Box (1)	2-track road at SE colony boundary
51	06/02/00	Shells (1)	Base of hill along NE colony boundary
	06/09/00	Shells (30)	Northern slope of hill along NE boundary
	06/27/00	Shells (1)	Top of hill along NE colony boundary
	07/03/00	Shells (4)	Top of hill along NE colony boundary
	07/10/00	Shells (64)	Base of hill in NE (<10 m from nest 50)
62	05/29/00	Dead Prairie Dog (shot through head)	Water tank in NW colony corner
	06/21/00	Shells (44)	2-track road along western boundary
	06/27/00	Shells (29), Recreational Shooter	2-track road along western boundary
	07/10/00	Shells (171)	2-track road (<100 m from nest 57)
	07/19/00	Shells (28), Shell Racks (3)	2-track road (near nests 57 & 58)
74	06/21/00	Shells (30)	2-track road east of water tank
76	05/24/00	Shell Racks (2)	Colony center
	06/04/00	Recreational Shooters (2)	Main road along northern colony edge
	06/14/00	Shells (1), Shell Rack (1)	Colony center
78	06/15/00	Recreational Shooters (2)	Walking east across colony